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THE BRITISH RUST FUNGI
(UREDINALES)



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THE BRITISH RUST FUNGI (UREDINALES)

THEIR BIOLOGY AND CLASSIFICATION

BY

W. B. GROVE, M.A.

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PREFACE

IT is now twenty-four years since the publication of Plowright's "Monograph of the Uredineæ and Ustilagineæ," and during that long period very great progress has been made in elucidating the biology of the former group. To Plowright will ever belong the honour of being one of the pioneers in this important work, especially in that branch which is the most fascinating and has the greatest number of secrets to unfold—viz. Heterœcism. But since his time numerous investigators have followed in his footsteps, while others have taken new ground and largely increased our knowledge, so that the picture which he presented of the biology and classification of the Rusts has now become, in certain directions, very incomplete and misleading.

The descriptions in the present volume are naturally based upon those in the "Monographia Uredinearum" of the brothers Sydow, so far as that monumental work has been published. Those of all the species of which British specimens could be procured have been carefully revised, and there is hardly one of them that has not been added to or amended. Fischer's "Uredineen der Schweiz," and McAlpine's "Rusts of Australia" have also been found extremely useful. No attempt has been made to give a full synonymy, but merely so much as was required to show the origin and authority of the name used, and to include all the references to the various species contained in the works consulted, especially those of Cooke and Plowright. Dates have been added occasionally, but only for special reasons or if the nomenclature adopted differs from that in the

"Monographia," where a complete synonymy, with dates, lies at the disposal of those who are interested in that matter.

A plan has been adopted, in a few cases, of grouping some forms that are closely allied under a common name; see *Puccinia dispersa* and *P. sessilis*. With more knowledge (or more courage) this process might have been carried much farther, and it is believed that in this device will be found the first line of defence of sane systematists against the excessive multiplication of "species" by "biological" nomenclators. It cannot be justifiable to use the same word in the same branch of science to denote two widely diverse grades of evolution. Physiological, unaccompanied by morphological, distinctions should never be allowed to constitute a difference of species, unless it be as a temporary measure in cases which have not been investigated.

In selecting the name for each species, the principle of priority has been followed, subject to two conditions—(1) names given to varieties need not be adopted (International Rules, 1905, Art. 49), and (2) names given to imperfect states are not to be preferred, but the earliest name given to the perfect (in this case, the teleutospore) stage (Brussels Congress, 1910); sometimes, however, the name *Uredo* may have included the perfect stage, as in some species of *Uromyces* (*U. Scirpi*, etc.).

Since æcidiospores are almost always "rounded-polygonal," their shape is not mentioned unless it deviates from this form. In the systematic part, all the spores are drawn to the same magnification (600 times), except where indication to the contrary is given. The drawings are all original and from British specimens, unless a different source is stated. When several similar spores are outlined, the surface-sculpture is not always indicated upon every one of them.

My thanks are especially due to Professor G. S. West, by whose advice this work was undertaken and by whose assistance it has been chiefly carried through. The 'Plowright' Herbarium of Fungi, which is in the possession of the University, has been

of considerable use, and the Principal (Sir Oliver Lodge) most kindly obtained for me a grant towards the cost of preparing the illustrations. By the courtesy of Dr A. B. Rendle, Keeper of the Botanical Department of the British Museum, and that of the Director of Kew Gardens, the Herbaria at those institutions have been consulted and much useful information has been derived therefrom. Thanks are also due, and are hereby gratefully tendered, to Herr H. Sydow (of Berlin) and Mr J. Ramsbottom (of the British Museum) who have both given unstinted help, to Mr T. B. Roe (a very successful collector of specimens), Professor A. H. R. Buller, Mr A. D. Cotton, Mr H. J. Wheldon, Mr C. Crossland, Mr J. Adams, Sir Frederick Moore, and many others in a smaller degree.

W. B. GROVE.

THE BOTANICAL LABORATORY,
UNIVERSITY OF BIRMINGHAM.
July, 1913.

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INTRODUCTION

THE Uredinales form a group of Fungi which is also spoken of as the Uredineæ or the Rusts. An accurate acquaintance with their nature is of great importance to the gardener, the forester, or the agriculturist, on account of the enormous loss which is caused by them every year and which can, at least in part, be avoided by a fuller knowledge.

All the species are parasitic, growing upon or in a living plant, which is called the *host*. The majority of the species of Uredinales have more than one stage of growth, distinguished by the form and arrangement of the spores which they produce; the number of distinct kinds of spores which a single species can possess varies from one to five. If the various spore-forms are all borne upon one host, the species is called *autoecious*. But it is a remarkable fact that a large number of the Uredinales pass their existence alternately upon two hosts, certain of the spore-forms being always produced upon the one, and the remainder upon the other. Such species are called *heteroecious* or metœcious. Many of those which grow upon grasses or sedges are probably heterœcious, though this has not been shown in every case, and there are a few proved exceptions. In order to convey a notion of the complex nature of the Uredinales, one of the heterœcious species will be taken as the type, and its various stages will be described.

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ADDITIONS AND CORRECTIONS

- p. 24. Fig. 225 should be Fig. 226.
- p. 28. Fig. 241 should be Fig. 242.
- p. 139. *Puccinia tinctoriicola* Magn. (Ester. Bot. Zeitschr. p. 491 (1902)) should be added as a synonym to *P. tinctoriae*.
- p. 150. *P. Leontodontis*. I have since found this species on *L. hirtus* (*Thrinchia hirta*).
- p. 238. *P. oblongata* has also been found on *Luzula silvatica*.
- pp. 296—7. It is stated that *Phragmidium violaceum* infests most of the subspecies of *Rubus fruticosus*, except those belonging to the group "Corylifolii," while *Ph. Rubi* is confined to that group and the allied *Rubus caesius*.

CHAPTER I

LIFE-HISTORY OF *PUCCINIA CARICIS*, THE NETTLE AND SEDGE RUST

Puccinia Caricis has two of its stages, the spermogonial and æcidial, on the Nettle (*Urtica dioica* and other species), and two others, the uredo- and teleutospore-stages, on various species of *Carex*, especially *C. paludosa*. The first appearance on the nettle is in the spring, about the end of April or the beginning of May, when small swollen yellowish spots can be seen on the upper surface of the nettle-leaves. These spots are round and convex above, sunken beneath, and about 3—4 mm. in diameter; soon they turn orange on the upper surface, owing to the development thereon of the *spermogones*, small flagon-shaped bodies walled in by a large number of slender orange hyphæ and filled with many hundreds of minute spore-like cells, the *spermatia*, which are orange in mass, though singly they appear colourless (Fig. 1).

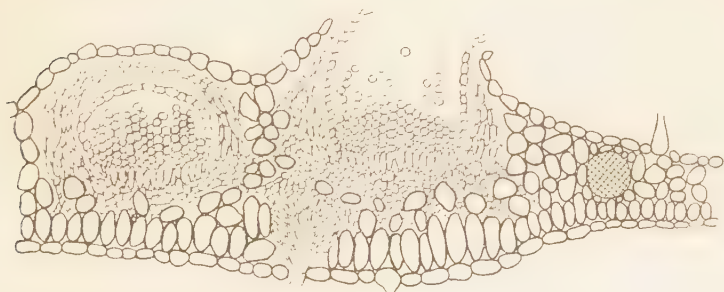


Fig. 1. *P. Caricis*. Section of leaf of Nettle, showing the hypertrophy produced by the mycelium of the æcidium-stage; a spermogone, on the upper side of the leaf, and two æcidia, one closed, on the under side. The upper face of the leaf is turned downwards. $\times 60$.

The mycelium in the leaf is strictly localised, forming little knotted masses (*plectenchyma*) just beneath the epidermal cells of the affected spot: all the cells of this mycelium are uninucleate. Some of these hyphæ turn upwards, remaining densely crowded and more or less parallel to one another, and enclose the flask-shaped cavity, at length converging to a point above it and piercing the epidermis at that place. Then the upper ends of these hyphæ diverge and form a brush-like bundle surrounding a narrow canal, or ostiole, which connects the cavity with the external air (Fig. 2). Meanwhile other hyphæ

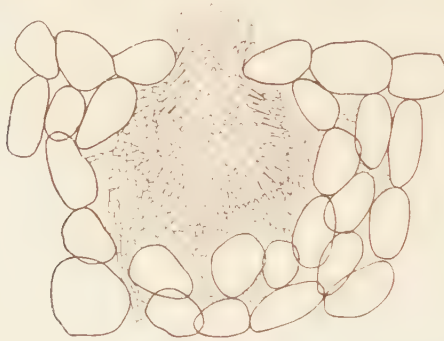


Fig. 2. *P. Caricis*. Vertical section of spermatogone, on leaf of Nettle. $\times 200$.

from the base have grown up within the flask, and made a lining to its lower half; these hyphæ are exceedingly delicate and numerous, and each abstricts from its end, successively, large numbers of the spermatia (Fig. 2), accompanied by a quantity of sugary mucilaginous matter which binds the spermatia into a coherent mass. The mucilage soon swells by imbibition of moisture, and the spermatia are forced out of the flask, through the ostiole, and form an orange globule between, and on the top of, the diverging hairs. Ultimately the mucilage dries up, or is washed away by rain, and the spermatia are dispersed.

The spermatia are very small, thin-walled, oblong or roundish cells, each containing a single relatively large nucleus, but little cytoplasm and no reserve material. When placed in a nutritive solution, they are capable of a kind of germination,

but the mycelium produced is very scanty. Their function will be discussed in a later paragraph, but it may be mentioned here that all attempts to produce infection by means of them have uniformly failed.

THE ÆCIDIUM.

Before the spermogones have completed their development, similar but larger conglomerations of hyphæ arise on the lower surface of the leaf, a little way below the epidermis, which they raise up into a rounded dome. These masses enclose a number of erect hyphæ of two kinds—an outer series of parallel closely-joined colourless hyphæ, forming the *peridium*, consisting of more or less hexagonal cells, which meet above and roof over the dome-shaped cavity; and an interior series which remain shorter and give off from their upper end parallel chains of spores called *aecidiospores*, which fill the whole of the enclosed space. Each new spore is produced beneath the older ones, which are thereby pushed gradually up. Finally, this structure, which is called an *aecidium*, ruptures the epidermis, forces its way between the cells, the *peridium*



Fig. 3. Leaf of Nettle (under side) showing the æcidia of *P. Caricis* on the lamina and petiole. $\times \frac{1}{2}$.

bursts at the summit, the edges become revolute, and there is formed a white cup-shaped hollow, its floor covered with erect chains of orange spores (see Fig. 1). These spores have a rather thin, colourless, finely warted cell-wall, and are filled with rich bright-orange granular and oily contents. The mycelium which forms the æcidia is continuous with that which bears the spermogones, and its cells are uninucleate, but the spores themselves are binucleate. The origin and meaning of this change will appear afterwards.

The oldest spores being at the top, they separate as soon as mature, and are blown away by the wind; fresh spores are produced for a time from below. Since these cups are in dense clusters over the whole of the affected spot, they are known as "Cluster-cups." The mycelium in the leaf continues to develop, and the spot enlarges and ceases to be round. But the swelling of the tissues within which the mycelium is living can be carried to such an extent as to distort and curl the leaf, much in the same way that *Econtseus deformatus* (the Peach Leaf-curl) affects the Peach leaves. The epidermis above and around the spot, also, often becomes coloured red or purple by an anthocyan-derivative, both these effects being a response by the leaf-cells to the stimulus of the parasitic growth, and perhaps part of an effort to throw off or checkmate the invader. The mycelium, moreover, is not confined to the leaves; it may originate in the petiole, in the stipules and in the stem. In the latter case it causes notable curvature and distortion; an instance is recorded where the curved gall-like mass, formed on the stem, measured as much as 10 cm. in length, and similar but smaller growths may frequently be met with.

Here should be noticed the close parallelism, up to a certain point, in the formation of the spermogones and the æcidia—they have similar shapes, they are both enclosed by a layer of sterile hyphæ, they arise in (usually) quick succession on the same mycelium, they give off basipetal chains of spores from their base. On the other hand, besides the difference in the nuclei, the æcidiospores differ from the spermatia in their larger size, in possessing a large store of reserve food, in their capacity for germination, and for producing infection in another plant.

THE ÆCIDIOSPORES.

The mode in which the æcidiospores are produced is as follows:—The upper cell of the sporiferous hypha usually divides into two, an upper sterile cell, and a lower fertile or basal cell, each with one nucleus. The upper cell disintegrates and perishes; the lower fertile cells conjugate with one another in pairs, the process consisting in the formation of a small hole

in the dividing wall which afterwards enlarges until at length hardly any trace of the wall is left. The two cytoplasmic masses thus form one mass, but the nuclei arrange themselves more or less side by side without fusing or in most cases even touching. This process must be regarded as an act of fertilisation or rather as a substitute for such an act¹. The double cell is called a fusion-cell.

The two adjacent nuclei are said to be "paired," and together constitute a *synkaryon* or *dikaryon*. Occasionally, in some species of *Puccinia* and other genera, these fusion-cells contain three nuclei, probably by a double fusion. Such cells produce trinucleate spores, but the fate of these is not known.

The paired nuclei of the fusion-cell then divide side by side and simultaneously—a process called *conjugate division*—and a wall is formed between the two pairs. The wall is formed in such a way that the two nuclei in the same cell are not sister-nuclei (see Figs. 19, 20).

The fact that in *conjugate division* the paired nuclei divide so that the two are usually in the same stage of mitosis at the

¹ The stages connected with the sexual process in general are three in number—(1) the association of two (almost always non-sister) nuclei in the same cell, (2) the fusion of the two nuclei, preparatory to (3) the reduction in the number of chromosomes, or at any rate in the amount of chromatin, to the previous ordinary vegetative condition. These three stages may or may not follow closely upon one another. The first and second, or the second and third, or the third and first, may be separated by an intervening series of cell-divisions. Which is to be regarded as the actual fertilisation? In all probability the first. The nucleus is the *director*, the cytoplasmic mass is the *work-people* of the *cell-factory*. The presence of the two *directors* is the essential fact. The fusion is of less importance; it is often delayed for a long period, and in certain cases it is known that, even when fusion has taken place, the chromosomes still retain their individuality for a considerable time. There is reason to believe that on the first introduction of fertilisation these three stages followed immediately (i.e. without intervening cell-divisions) after one another, the series of vegetative divisions being intercalated between (3) and (1), as in *Coleochaete* (Allen, 1905) and *Spirogyra* (Tröndle, 1907; Karsten, 1909). In the majority of the higher plants, stages (1) and (2) occur without much or any interval, but a long series of divisions (the sporophyte) is intercalated between (2) and (3). In most of the Uredinales, the chief series of vegetative divisions is intercalated between (1) and (2), and (3) follows immediately after (2). In certain Algæ (*Griffithsia*, *Dictyota*) the intercalation takes place on an extensive scale, both between (2) and (3) and between (3) and (1).

same time, shows that they mutually influence each other, and implies that all the cell-processes which go on are likewise under their common control.

The upper cell, cut off from the fusion-cell, is the æcidiospore-mother-cell: the lower grows a little longer and then divides again in the same way, and thus a vertical series of



Fig. 4. *P. Caricis*. Chain of young æcidiospores. 500. *a*, fusion-tissue; *b*, basal (fusion) cell, with conjugate nuclei; *c*, æcidiospore-mother-cell; *d*, intercalary cell; *e*, young æcidiospore.

æcidiospore-mother-cells is formed, the oldest at the top. Each of the æcidiospore-mother-cells, as soon as produced, cuts off, by conjugate division, a small cell below, called the *intercalary cell*; this soon becomes disorganised and disappears, while the other portion becomes the *æcidiospore*. Thus the chain at first consists of alternations of æcidiospores and abortive spores, both containing two nuclei (Fig. 4); the function of the latter may be, by their disintegration, to enable the æcidiospores to separate more easily from one another, and thus to aid dispersion by the wind.

The *peridium* is composed of cells homologous with the spore-mother-cells. They arise from basal cells containing two nuclei in exactly the same way; occasionally even an intercalary cell is cut off, but it does not disintegrate. All of them thicken their

walls and remain in close contact with one another; ultimately their contents disappear (Fig. 5). The central part of the dome-shaped peridium is composed of the terminal cells of the central spore bearing hyphae: they are probably less closely connected with one another, and the peridium ultimately bursts at that point.

The spores, if placed in a damp atmosphere, germinate readily when mature and fresh. Only those spores which are at the top of the chains and can be shaken out easily by

tapping are mature enough to germinate, and even they, owing to their thin walls, may lose this power in a few days according to circumstances. Especially can they be killed by rapid

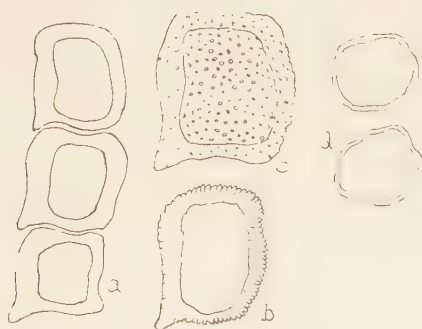


Fig. 5. *P. Caricis*. *a*, three cells of the peridium, on Nettle; *b*, a cell in optical section; *c*, the same in surface-view; *d*, two aecidiospores. $\times 600$.

drying. Instances are known, however, where some of them, kept in a cool place, retained their capacity for germination about seventy days, though most of them were dead after eighty days.

Each spore has a number of germ-pores; in *Puccinia Caricis* the number is about five or six; in other species of Uredinales the number varies from two to eight. These pores, which are scarcely visible until germination begins, are thin places in the inner layers of the outer wall, the whole cell bearing a close resemblance to many kinds of pollen-grains (microspores). (Fig. 6.)

It is worthy of notice that in the spores of *Endophyllum*, and others of the less advanced type, there are no real germ-pores; the germ-tube merely forces its way out at the first place that gives way. From this state of things there is a gradual transition from numerous to few germ-pores; in the highest types of all (*Uromyces* and *Puccinia* teleutospores), each cell has one and only one well-defined germ-pore.



Fig. 6. Aecidiospore of *P. Caricis*, germinating in water. $\times 180$.

The germ-tube of the acidiospore of *P. Caricis* can grow to a length ten or twenty times greater than the diameter of the spores, and often executes, at least in water, a number of spiral turns (Fig. 6): it remains nearly of the same diameter throughout, or may bear short stumpy branches here and there. The granular contents of the spore travel along the tube with its growth, remaining always towards the distal end. But unless the germinating spore has fallen upon its proper habitat, the leaf of a *Carex*, its attempt at growth comes to an end when its reserve-material is exhausted.

If, however, the spore has fallen upon a *Carex*, its germ-tube travels over the surface until it reaches a stoma, through the pore of which it enters the respiratory chamber, forms a swelling just inside as a kind of hold-fast, and then begins to branch and traverse the intercellular spaces, occasionally sending



Fig. 7. Haustorium of *P. Caricis* in chlorophyllose cell; *m*, mycelium; *h*, haustorium; *n*, nucleus of cell. $\times 500$.

an *haustorium* into the mesophyll-cells (Fig. 7). The cause of its entry is probably the search for water-vapour, since the germ-tube of a Uredine is found (De Bary, 1863; Gibson, 1904) to enter the stomata as freely on another leaf as on one of its proper host-plant, and also to pass through a hole, comparable in size to stomata, in a thin india-rubber membrane which separated it from air saturated with water-vapour (Balls, 1905).

But its further growth is influenced by chemotaxis of a more complicated nature: unless the right kind of stimulus is

furnished by its host, it cannot form effective haustoria, development is poor and abnormal, and death soon ensues (Gibson, 1904). The resistance of the host to the parasite, shown perhaps by the secretion of destructive enzymes, has also to be considered. Once inside the stomatal chamber, however, the fungus is largely protected from outside influences, such as desiccation: this preservative habit has no doubt contributed much to the wide-spread prevalence of the Uredinales.

THE UREDOSPORES.

The germ-tube soon forms a more or less extensive mycelium, which may penetrate the greater part of the leaf of the *Carex*, but in many species of *Puccinia* is strictly localised to a small defined spot. All its cells are binucleate, like the spore from which it originated. The cells of the mycelium, in every stage, send *haustoria* into the cells of the host; when an haustorium arises from a binucleate mycelium, it is itself

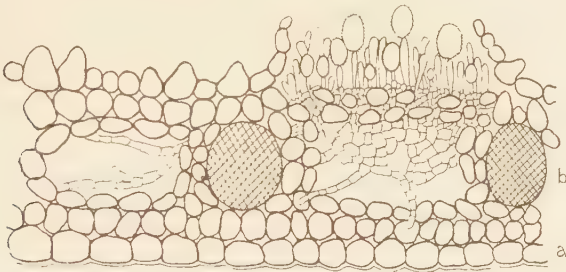


Fig. 8. Section of leaf of *Carex paludosa*, with a sorus of uredospores of *P. Caricis*; a, upper epidermis; b, a vascular bundle. Most of the pedicels have lost their spores. $\times 180$.

likewise binucleate. After a few days this mycelium begins to form the third kind of spore—the *uredospore*. A knot of hyphæ is formed just beneath the epidermis; some of the branches turn upwards and form a regular layer parallel to the surface—the *spore-bed* (Fig. 8).

The upper rounded cell of each hypha is divided into two daughter-cells, the lower of which is developed into a stalk, the upper becomes the uredospore (Fig. 9). The spore is oval or roundish; when mature it is enclosed in a double cell-wall, the outside being cutinised and provided with spine-like projections, somewhat like those of the æcidiospore, only more pointed. In the inner layers of the exospore there are usually three (rarely



Fig. 9. *P. Caricis*. Developing uredospore (1, 2, 3, 4, show stages of growth; 5 is a pedicel from which the spore has vanished). $\times 500$.

four) germ-pores: in fact, the uredo- resembles the acidiospore in character, and must be considered as homologous with it—the stalk-cell corresponding to the *intercalary cell* of the latter. But they differ considerably in the fact that the uredospore is

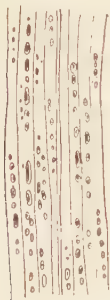


Fig. 10. Leaf of *Carex pendula*, with uredo- and teleuto-sori, slightly enlarged.

always produced singly, not in chains. (This is not true, however, of all the Uredinales.) The membrane of the uredospore is nearly colourless, but it encloses a bright orange granular and oily mass, with two nuclei. Every cluster of uredospores produced on the same spore-bed is called a *sorus*; it is surrounded by the laciniae of the epidermis, which is more or less torn or split by the enlarging mass. In many cases, several sori become confluent and form a larger pustule (Fig. 10).

In other species of Uredinales the uredospores have coloured membranes or possess a larger or smaller number of germ-pores. Moreover the distribution of these pores over the surface is characteristic for each species: they may be placed equatorially, as they are in *P. Caricis* (Fig. 11), or towards the poles, or scattered over the surface with regularity or without any order.

A uredospore may be very easily detached from its pedicel, and conveyed (chiefly by wind, though sometimes by insects)



Fig. 11. A uredospore which has germinated, showing the three germ-pores. $\times 600$.

to another leaf of *Carex*, on which it germinates, the germ-tube enters a stoma, produces a fresh crop of mycelium and another sorus of uredospores; this process can be repeated indefinitely. The mycelium can also grow up and down the leaf, producing fresh sori in its course; for this reason the sori are usually arranged in linear series, owing to the

parallel venation of the *Carex*-leaf. The germ-tubes of the uredospores are often curled or branched like those of the acidiospores, and the germination is of the same character in

both (Fig. 12). The uredospore retains its capacity for germination for a longer time, even for more than three months; in fact, in certain foreign species, some of these spores acquire a thicker wall which enables them to act as a kind of resting-spore—these are called *amphispores*, but they are not formed by *P. Caricis*.

It is found, generally, that if the spores of the Uredinales are dried gradually, they retain their power of germination for a longer time and in a better degree than if dried quickly or not dried at all. Most likely a slow drying enables them to mature more perfectly.



Fig. 12. Two uredospores of *P. Caricis*, both germinating in distilled water. $\times 180$.

THE TELEUTOSPORES.

After a time, probably in response to the weather or other change of environment, the mycelium which has hitherto given rise only to uredospores begins to produce, at first in the same, afterwards in separate sori, the fourth kind of spore—the teleutospore. In the genus *Puccinia* this is almost always a compound body, formed of two superposed cells; each cell is really a spore, and is capable of independent germination. In many species of the genus the teleutospores readily break apart at the septum, e.g. in *Puccinia fusca* and *P. Prunispinosae*, and the lower half may be, and has been, mistaken for a uredospore. Those of *P. Caricis* do not easily break apart until they are old and dead.

The teleutospores are formed on a pedicel, much in the same way as the uredospores, except that the uppermost cell is again divided, but apart from that they differ widely in their character. They have a thick dark-brown exospore, covered with a chitinous cuticle; in this species the exospore

is much thicker at the apex than elsewhere (Fig. 13). While the spores are standing in a densely crowded sorus, the apex is the part most exposed to the weather, and therefore most needing protection. There is a thin endospore to each cell: the contents are granular and at first oily: there is a large and conspicuous nucleus in the centre of each. This nucleus, in its resting stage, is almost homogeneous except for its nucleolus, and was mistaken by the older observers for a "vacuole."



Fig. 13. Teleutospore of *P. Caricis*. $\times 600$.

Since the mycelium from which the teleutospores, as well as the uredospores, were formed contains paired nuclei, the cells of the teleutospore were at first in the same condition. When its wall, however, begins to thicken, i.e. when it is becoming mature, the conjugate nuclei unite, and form one large fusion-nucleus (Fig. 14). The two fusing nuclei, after the very

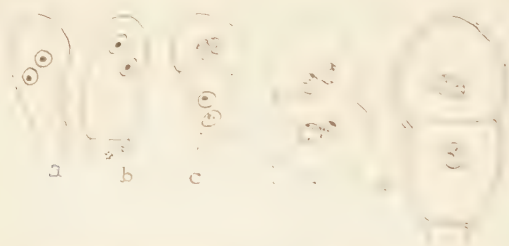


Fig. 14. Formation of teleutospores of *P. Falariae* (after Dittschlag): *a*, the spore-bearing hypha; *b*, the same divided into pedicel and spore-cell; *c*, the spore divided into two cells; *d*, a young teleutospore; *e*, the same after the fusion of the nuclei. $\times$ about 800.

numerous conjugate divisions during the long period of growth from the formation of the fusion-cell of the æcidium, would be related, as it were, like very distant cousins, especially since the nuclear divisions during this period, though indirect, appear to show a very simplified form of mitosis, tending rather to be of the nature of amitosis. The fusion, as already intimated, is not to be considered as the act of fertilisation, but merely as a necessary preliminary to chromatin-reduction.

It is in the germination of the teleutospore, presently to be described, that its most distinctive feature is to be found. The chief function of teleutospores is to act as resting-spores, and in the majority of cases they will not germinate until they have passed through a period of quiescence; in the present instance this period is the winter, but it is not necessarily always so. The resting-spore is primarily a device to tide over an unfavourable period—whether of food-supply, moisture, temperature, or resistance of host—without regard to season. Some species, however, have teleutospores which can germinate immediately, as in *P. Malvacearum*; those teleutospores usually have thin walls. *P. Malvacearum* is sometimes supposed to hibernate by a perennial mycelium, but there is reason to believe that in most cases infection each year proceeds from over-wintered teleutospores. Most of the species which have these thin-walled spores also produce some with thicker walls, which act as resting spores in the ordinary way.

Besides the two-celled teleutospores, several species of *Puccinia* also produce similar spores with only one cell—these are called *mesospores*. A mesospore can occasionally be found in many *Puccinias*, even in *P. Caricis* (Fig. 15), but in others they are abundant, e.g. in *P. Porri*, where careful search is often required before a two-celled spore can be detected. Mesospores arise merely by the omission of the last nuclear division; they are exactly of the same nature as the two-celled teleutospores and germinate in the same way. By this means they can be distinguished from the amphispores previously mentioned, but not of course from the teleutospores of *Uromyces*. In fact authors have described some species which produce them as *Uromyces*, overlooking the rarer two-celled spores that occur with them. See remarks under *Puccinia Porri* and *Uromyces ambiguus*.



Fig. 15. A mesospore of *P. Caricis*. $\times 600$.

GERMINATION OF THE TELEUTOSPORE.

We now approach the consideration of a process which has been in the past much discussed, and upon the right interpretation of which the whole question of the systematic position of the Uredinales depends. Each cell of the teleutospore of *P. Caricis* has one germ-pore, though some genera allied to *Puccinia* have teleutospores with more than one germ-pore to each cell, e.g. *Phragmidium*, *Uropyxis*, *Calliospora*. The germ-pore of the upper cell is in the thickening at the summit, that of the lower cell is lateral and just beneath the septum. Each of these pores is a canal passing through the cell-wall, and covered only by the cuticle. Through these pores the germ-tube passes, first appearing as a roundish swelling, the protoplasm being surrounded by the thin endospore. This then elongates, the nucleus squeezes through the relatively narrow pore and

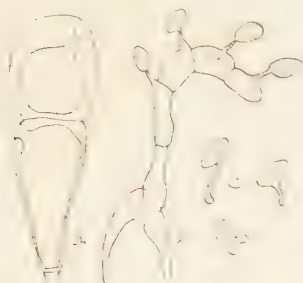


Fig. 16. *P. Caricis*. *a*, a mature teleutospore; *b*, upper cell of same, germinating and forming a basidium; *c*, basidiospores germinating. $\times 600$.

enters the tube where it divides twice, and forms four superimposed cells, separated by thin cell-walls (Fig. 16). This row of four cells was formerly known as a *promycelium*, but is now called a *basidium*. If kept in water these cells can round off and separate from each other¹, and germinate by sending out a tube, like the mycelial cells and spores of many fungi. But if in a damp² atmosphere, each cell without

separation produces a sterigma at the end of which a *basidiospore* is formed, like the basidiospores of Agaricini. These basidiospores can germinate at once, even before they are detached from the sterigma, by sending out a short tube which may produce a *conidium* resembling the basidiospore at its end.

¹ This method is said to take place normally in *Barclayella*.

² It is noted by many observers that, in a state of nature, it is a layer of dew, not of rain, that is favourable to germination.

If one of these easily detached basidiospores or conidia is conveyed to the surface of a leaf or young stem of Nettle, its germ-tube bores through the cuticle and enters the tissues (Fig. 17), where it ramifies and forms a mycelium. The teleutospore is large and heavy, and firmly attached to its spore-bed on the leaf of *Carex*; the basidiospores enable its contents to be transferred easily to the surface on which alone they are capable of further growth. But their wall is thin and they can live only for a short time; they contain but little food-supply and could not form a long germ-tube. That is the reason why their germ-tubes do not, like those of the other spores, search for a stoma, but enter by the quickest means. Nevertheless they can abnormally enter by a stoma; De Bary records such a case in his account of *P. Dianthi* (see Fig. 24).



Fig. 17. *Endophyllum Sempervivi*. Germinating basidiospores (after Hoffmann); s, the spore; v, the germ-vesicle, under the cuticle of the epidermis; a, b, c, show the passage of the spore-contents into the vesicle. $\times$ about 200.

The germination of the teleutospores of *P. Caricis* takes place about the second week in April, and on the mycelium produced by the basidiospores in the nettle there arise, in about a fortnight, first spermogones and then æcidia like those with which we started. But the mycelium arising from the basidiospores does not always proceed immediately to spore-production. In some species, e.g. *Endophyllum Sempervivi*, it hibernates in the growing point of the shoot, or in the leaves if they are evergreen, as in *Puccinia Buxi*, or in the stems or branches in the case of some that live on shrubs or trees, as in *Cronartium ribicola*.

Rather more than a twelfth of the species of Uredinales are now known to be heterœcious. This mode of life may be regarded partly as a device by which the parasite tides over the time during which one of the host-plants is not available. The leaves of the Nettle are delicate and soon perish in the autumn; those of the Sedge persist throughout the winter. The power of heterœcism increases the ability of the fungus to

adapt itself to new conditions and thus tends to perpetuate the race, while the change of host, which is equivalent to a change of diet, may very possibly tend to an increase of vigour in the individual.

The former statement, however, must not be taken to refer to all cases of heteræcism, since there are instances, e.g. in species of *Coleosporium*, which cannot be explained on this ground.

The reason why *P. Caricis* has been taken as the typical Uredine, instead of the usual *P. graminis*, is that the æcidium of the latter is now very rarely found in this country and is therefore not available for demonstration, while that of *P. Caricis* is common in all suitable localities. Even if not existing in any place, it can be readily introduced if the three prerequisites are at hand:—a pond bordered by *Carex paludosa* and by *Urtica dioica*, and also a quantity of the leaves of *Carex* infested by the parasite. The Nettle and the Sedge are not injured appreciably by the disease, nor would it be of much consequence if they were. To introduce the fungus into the new locality, it is only necessary to obtain a bundle of the required leaves (say about 500) from some place where the *Puccinia* exists, in January or February, and lay them on the ground where a patch of nettles is known to occur. The latter will be seen in spring to be beautified by the æcidium, and in the summer the disease will spread to the surrounding sedges (see Grove, *Journ. Bot.* 1913, p. 42).

CHAPTER II

THE SEXUALITY OF THE UREDINALES

De Bary suggested in 1884 that, if there was any sexual act occurring in the life-cycle of the Uredinales, it would probably be found in connection with the æcidium. At that time nothing was known on this point, and De Bary anticipated that something might take place analogous to what happens in the formation of the asci of certain Ascomycetes.

The first discovery was made by Blackman (1904), who found that, in laying the foundation of the spore-bed of the æcidium of *Phragmidium violaceum*, cells became binucleate by the passing into them of a nucleus from an adjoining vegetative cell. He saw that this passage took place through a narrow opening formed between the cells (Fig. 18). The binucleate cell then became the equivalent of an oospore, and formed the beginning of a sporophytic generation. In other words, he supposed that the fertilised cell represented a female gamete and the vegetative cell replaced a now vanished or functionless male gamete. The fertilisation would then be of the nature of a *semi-apogamy*. He considered that the spermatia were the functionless male gametes. From the cell to be fertilised he saw an upper sterile cell cut off, which soon

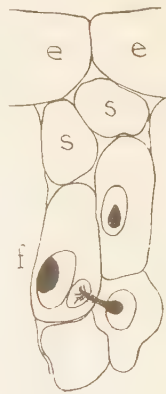


Fig. 18. *Phragmidium violaceum*. Development of æcidium (after Blackman); *e*, the epidermal cells; *s*, sterile cells; in the basal cells below, a nucleus is seen migrating into a fertile cell, *f*.

degenerated; this he considered to represent an abortive trichogyne, in accordance with De Bary's anticipation. The acceptance of this interpretation implies the existence of a close affinity between the Uredinales and the Red Seaweeds.

In 1905, Christman published the result of his researches into *Phragmidium speciosum*, *Caeoma nitens* (= *Gymnoconia* = *Puccinia Peckiana*), etc. According to him, the process that took place was the fusion of the contents of two equal and similar gametes, with the exception that the nuclei remained side by side unfused. A considerable portion of the wall between the two fusing cells was broken down, and the process was of the nature of a conjugation, not a fertilisation.

Blackman and Fraser (1906) next examined a number of other species, and in *Melampsora Rostrupii* they found the same process which Christman had observed, though they still considered that other species, e.g. *Puccinia Poarum*, showed instances of the migration of a nucleus as in the first subject studied.

Christman, in 1907, showed that a similar act of conjugation between two equal cells takes place in the formation of the primary uredospores of *Phragmidium Potentillae-canadensis* (= *Kuehneola Tormentillae*, Arthur, q.v.), the primary uredospores in this species replacing the æcidium which is absent.

In 1908 Olive, in examining the primary uredospores of *Triphragmium Ulmariae*, tried to reconcile the difference between these opposing views: he considered that conjugation took place between two cells, one larger and one smaller, and that either a large opening was formed so that the two protoplasts fused, or a narrow hole was produced through which the nucleus of the smaller cell passed into the larger. He considered the upper sterile cell as a degenerating tip-cell, not an abortive trichogyne. The fusing cells might be placed in almost any position with respect to each other. In *Puccinia transformans*, a *micro-form*, possessing only teleutospores, he shows that the basal cells which produce them arise equally by the fusion of two uninucleate cells.

Kurssanow, in 1910, investigating *Puccinia* (*Gymnoconia*) *Peckiana*, found both cases that of Blackman and that of

Again, in 1911, Hoffmann investigated a Uredine of a lower type than most of those previously considered, viz. *Endophyllum Sempervivi*. This genus differs from all the other Uredinales in its mode of development. It has only spermatia and æcidiospores, the latter functioning also as telentospores in that their conjugate nuclei fuse, and then on germination they produce a basidium and basidiospores. These basidiospores reinfect the host and produce both spermogones and æcidia. On the spore-

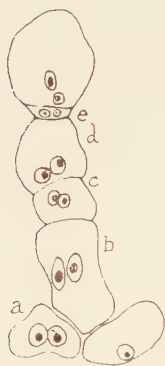


Fig. 21. *Endophyllum Sempervivi*. Formation of æcidio telentospores (after Hoffmann). *a*, fusion-tissue; *b*, basal cell; *c*, intercalary cell; *d*, spore; *e*, intercalary cell, degenerating.

bed of the æcidium two adjacent cells unite by the dissolution of the intervening walls (Fig. 21); first a small hole is formed, which grows larger until at last almost no trace of the wall is left. The disappearing wall is often horizontal, not vertical as in most of the other cases, and the conjugating cells are not situated in any definite plane. In such cases a sterile (trichogyne) cell was not seen.

Finally Fromme (1912) found that in *Melampsora Lini*

the spermogones and æcidia are produced simultaneously and only from infection by basidiospores. The spermatiophores differ from all others described in being many-celled, each cell producing a single spermatium on a sterigma-like process; they arise from a regular layer of large rectangular cells at the base of the spermogone. The æcidia are stated to be undistinguishable from the spermogones externally, but produce female gametes in the usual way, generally with one or two "buffer" cells which speedily disintegrate. The female gametes conjugate, in abundance, laterally in pairs, often in threes or fours; the fusing cells are of equal rank, but need not be in the same horizontal level. Æcidiospores were observed with several nuclei, and one æcidiospore-mother-cell was seen with as many as eleven nuclei. (See also note on p. 29.)

From a comparison of all these observations it now becomes certain that, in the Uredinales, the typical mode by which the binucleate condition arises is by the conjugation of two similar cells, each provided with a large nucleus and an abundant supply of food. This fusion-cell can afterwards branch by the formation of lateral buds, usually in basipetal succession, and may thus produce several rows of spores at once; by a similar branching *bunches* of uredospores and teleutospores can arise in the sori of those spore-forms (Blackman, '06, Christman, '07, Dittschlag, '10, Hoffmann, '11). See Figs. 37, 156.

At first, it may be supposed, the two conjugating cells belonged to a definite basal layer or spore-bed, as in *Phragmidium*, *Puccinia* spp., and *Melampsora Rostrupii*; but afterwards they ceased to be arranged in a layer, and conjugation took place between two purely vegetative cells in the mycelium beneath. The beginnings of this change are seen in *M. Rostrupii*, and its final product in such *micro-forms* as *P. Adorae* where the greater part of the mycelium has synkarya.

Whether the upper sterile cell which is so frequently met with is to be considered as an abortive trichogyne is not so certain. But it may be remarked that, since the sori generally arise beneath the epidermis, no fertilisation could have taken place by non-motile spermatia unless there were something of the nature of a trichogyne to protrude through a stoma. In this connection it is important to remember that in *Uredinopsis*, one of the lowest of the Uredinales, the sori of primary uredospores, i.e. æcidiospores, seem always to arise beneath a stoma; other sori can arise in many genera in the same way, and in the genus *Hemileia* the pedicels of the uredospores protrude into the air through the stomatal pore. Moreover we know that, while æcidia of the enclosed higher types, as in *P. Caricis*, arise at some depth in the host-tissues, and the basal layer and its peridium are covered by a considerable thickness of dead empty cells (which are afterwards pushed to the sides), the æcidia of the more primitive form, the cæoma type, are shallow and are not enclosed in a peridium, but are either quite naked or surrounded only by a few paraphyses.

In the typical Uredinales, the conjugation of the two

(female) cells takes place just before the formation of the æcidium or its representative: in the reduced *micro-* and other forms, such as *P. Adonis* and *Uromyces Scillarum*, it is probable that the conjugation of the two (vegetative) cells takes place at some more or less indefinite period before the formation of teleutospores.

There is a general agreement among investigators that a structure resembling an ascogonium (from which the mass of basal cells may be supposed to originate) does not exist in the Uredinales, notwithstanding the suggestions to that effect by Masee (1888) and Richards (1896). If it did exist, or had existed, it would do something towards accounting for the definiteness in form usually presented by an æcidium; if it is totally unrepresented, the æcidium cannot be regarded as a morphological unit, but only as a collection of female cells. It is possible that traces of its existence are shown by the large multinucleate cells, containing 12—15 nuclei, which have been described by Olive (1908) in the mycelium at the base of the young æcidium of *Puccinia Cirsii-lanceolati* and by others at the base of teleuto-sori, but this question must remain open till further investigations are made. The existence of an ascogonium of that kind would, of course, be inconsistent with the trichogyne-interpretation of the sterile tip-cell in the æcidium.

Æcidiospore-mother-cells and æcidiospores with three or even more nuclei are frequently met with; these represent the result of a fusion of three or more cells of the spore-bed. But since uredospores and teleutospores with cells containing more than two nuclei seem to be unknown, it is probable that these abnormal æcidiospores undergo no further development.

THE NATURE OF THE SPERMATIA.

There are two and only two possible interpretations of the spermatia—either they are male gametes, or they are conidia, i.e. merely additional multiplicative spores like the uredospores. In favour of the former view the following arguments can be adduced:

- (1) *The time of their appearance*, just before the formation

of the æcidium or its representative, and on the same mycelium. For instance, in those cases where there is no æcidium, but primary uredospores which are formed, like æcidiospores, from a fusion-cell, followed by secondary uredospores which are not so formed although similar in all other respects—then the primary spores *alone* are accompanied by the spermatogones. This argument is the most decisive.

(2) *Their size and character.* They are much smaller than the other spore-forms, with thin walls, a large and not very degenerate nucleus though often without a nucleolus, little protoplasm and no reserve-stuff (oil, etc., with which the ordinary spores of the Uredinales are so richly provided), thus reminding one of the spermatia of the Florideæ.

Sharp (1911) reports, in *Puccinia Podophylli*, spermatia three times as long as the nucleus, and therefore containing some appreciable amount of cytoplasm. But protoplasm is not reserve-stuff.

(3) *They will not reproduce the species.* All the efforts that have been made to cause them to do so have uniformly failed. All the other reproductive cells of these Fungi can be successfully used for that purpose, if applied to the proper host. In some species, as *Cronartium ribicola*, the spermatia can be collected in large quantities: Klebahn made numerous trials with them, but entirely without result. Jaczewski and others have confirmed his experience. It is a commonplace observation that highly specialised male cells cannot in themselves reproduce the species, while female cells can, as in the cases of parthenogenesis, both true and false. This difference in behaviour is partly correlated with the difference in the amount of food-reserve available, with which the larger female gametes are usually well supplied. In conjugation, where the two (male and female) gametes are approximately of equal size (as in certain Mucorini), each may form a functional azygospore.

(4) *They will hardly germinate* in water, probably because they have no reserve-food. If food is supplied by cultivating them in nutrient solutions, a little growth is obtained, but it is very insignificant and soon perishes. The same thing is true of male cells in other organisms. Conidia, under such

circumstances, would show quick and luxuriant growth: they cannot be degenerate conidia, because the nucleus is large and well-formed though at times no nucleolus can be seen.

(5) They are sometimes *accompanied by a sweet fluid*, which gives off a pleasant, or more rarely an unpleasant, smell, as in *P. suaveolens* (*obtegens*), *Uromyces Pisi*, *Cronartium Quercus*, etc. It is said that, in Japan, children lick the abundant spermatogones of *C. Quercus* on account of the sweet juice that oozes from them. The presence of this can be readily understood, if the aid of insects is invoked as well as wind, in order to carry the passive spermatia to the trichogyne projecting through a stoma, but otherwise is without explanation. The larva of a fly (*Diplosis*) or a similar organism, is to be found crawling about the leaf and feeding on the spermatia and æcidiospores of many Uredinales: its body is quite orange in colour through being filled with them, and the spermatia would adhere to its outer surface. Though the spermatogones of *P. Caricis* are usually on the opposite leaf-surface to the æcidia, yet in very many species they occur intermixed, and not infrequently the æcidia grow habitually in circles round little groups of spermatogones; a remarkable instance is seen in *Phragmidium Rubi-idaei* (= *P. gracile*); see Fig. 225.

(6) The most likely theory of the evolution of the Uredinales is that which places the majority of the *micro-* (including the *lepto-*) forms as the most recent.

It is just in these, and in no others, that the spermatogones are least often to be met with (see p. 39), as would be expected if they are furthest in descent from the primitive forms in which a true act of fertilisation occurred.

(7) If, on the other hand, we look upon the spermatia as conidial forms, *i.e.* as merely an additional means of vegetative multiplication, we are confronted by this difficulty (as well as those referred to above) that they appear just at that period of development at which they are least wanted, whilst they are missing in many *micro-*forms where additional help would be most welcome. The æcidiospores have been shown in many ways to possess an unusual amount of vigour and to be able to produce a stronger infection than the uredospores, which stand

next in order. Even, therefore, if the spermatia could produce an infection, their feeble aid would be wasted at such a time of rejuvenation.

(8) There is also to be considered the fact that the spermogones and spermatia of the Uredinales resemble those of the Collemaceæ, which have been shown by Stahl (1877) and Baur (1898) in all probability to fulfil the male function¹. It may be pointed out, in this connection, that the great similarity of the spermogones to the pycnidia of the Ascomycetes has been too much ignored, and that its significance is not yet fully appreciated. In the Ascomycetes the pycnospores in most cases undoubtedly act as conidial forms, and have lost all traces of their primitive male function—in the Uredinales the spermogones have equally lost their function, but have not taken on the secondary rôle of conidia: it may be suggested that the latter are otherwise well provided for in that respect, and hence feel no necessity for additional conidia. The spermatia of *Polystigma rubrum* are, however, functionless either as male cells or as conidia (Blackman and Welsford, 1912).

NUCLEAR DIVISION IN THE UREDINALES.

This is always of a simple type, not primitive, but reduced. The number of chromosomes seems to be always somewhat uncertain, and the chromatin forms masses which vary in number from one to four. In the ordinary vegetative division, which may be regarded as approaching rather to the nature of amitosis, the nuclear membrane disappears, the nucleolus is extruded, and the chromatin masses are drawn apart on a kind of rudimentary spindle to form the daughter nuclei. In *synkarya*, the two paired nuclei in a cell are almost always in the same stage of division at the same moment, and the four resulting daughter nuclei move apart in such a way that the two nuclei in each daughter cell are never sister-nuclei (Hoffmann, 1911).

¹ A remarkable instance in *Collema*, though outwardly not at all resembling the case of the Uredinales, is described by Bachmann (1912).

In the teleutospore (i.e. tetraspore-mother-cell), the first division is of a slightly higher type. The fusion-nucleus is large, round and (when unstained) perfectly clear and homogeneous, but for its nucleolus, so that it looks like a vacuole: it occupies almost invariably the middle of a cell. The dense chromatin mass is loosened out into a kind of spireme which becomes shorter and thicker; the nuclear membrane then disappears, and the spireme thread splits longitudinally, though the splitting is often indistinct. It then divides transversely into segments which become arranged or strung out on a spindle (sometimes, but more rarely, in an equatorial plate): then the daughter nuclei are formed at the poles, and the next division, which is homotypic, follows immediately (Harper and Holden, 1903; Blackman, 1904). Hoffmann considered that in *Endophyllum Sempervivi* he could count eight chromosomes just before the reducing division.

Since each of these nuclear divisions of the teleutospore-contents is usually followed at once by the formation of a cell-wall, there are obtained four cells which are generally superposed in a row. But Weir (1912) records a case in *Coleosporium Pulsatillae* where they were arranged in a "tetrad," by which word he means presumably (for he gives no figures) in a square or tetrahedral manner.

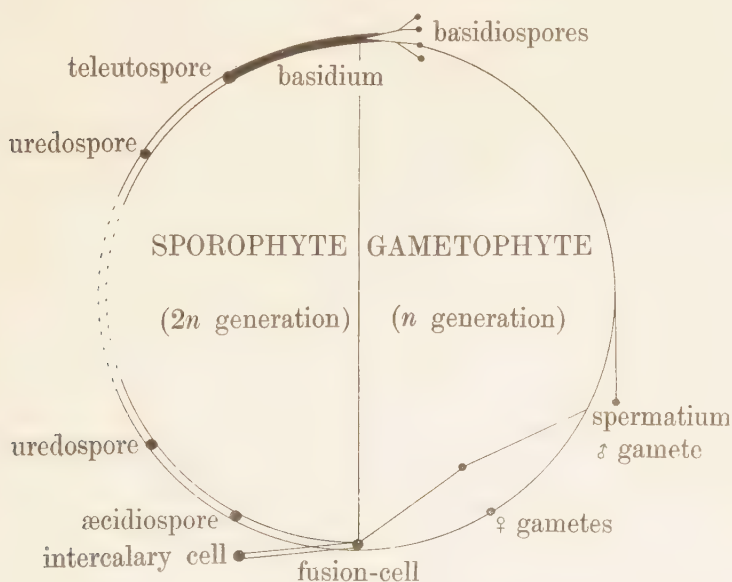
According to Dittschlag (1910) the nucleus of the spermogonial hyphae is oblong and shows a slight chromatin network, but usually without a nucleolus. After abstriction (for which see Blackman, 1904), each nucleus enters again upon a resting stage, and the chromatin network becomes looser. Each spermatium has a rather large nucleus, occupying about two-thirds of the cell, showing a decided chromatin network, but almost never a nucleolus. It has been frequently noticed that many spermatia soon become binucleate, but the nuclei are sisters, and this condition is merely a beginning of vegetative growth which, however, usually aborts.

In the acidia, the "fertile" (female) cells have a medium-sized nucleus, with a fine chromatin network and a deeply colouring nucleolus, as well as abundant finely granular protoplasm. When the conjugate nuclei have arisen, they lose their

nuclear membrane, the chromatin in each falls together in little masses, the nucleolus lying by the side of the mass: these then separate, a spindle is formed with an equatorial plate and the chromatin masses pass at different rates towards the poles. The nucleoli then disappear, and four chromatin balls are formed which are the daughter nuclei. Only after this is completed, do they separate into two pairs, and the formation of a cell-wall begins (Dittschlag).

THE ALTERNATION OF GENERATIONS.

Assuming, as we are now justified in doing, the truth of the foregoing ideas, we may represent the alternation of generations in a typical Uredine by the following diagram:



The n generation is that in which the nucleus has the haploid number of chromosomes or, if there are no distinct chromosomes visible, the single amount of chromatin; in the $2n$ generation each cell has the double (diploid) number of chromosomes or the double amount of chromatin, at first surrounded by two nuclear membranes, afterwards by one.

The teleutospore-cell is a spore-mother-cell, exactly comparable with a tetraspore-mother-cell. The "basidium" is merely the same cell, removed outside the old outer cell-wall for the convenience of the ensuing processes: in *Coleosporium* this removal does not take place, but the "basidium" is formed internally, the mucilaginous nature of the cell-walls of the teleutospores of that genus allowing the sterigmata to protrude through them (see Fig. 241), which could not be done through the hard cutinised cell-walls of the teleutospores of *Puccinia Caricis*.

The first division of the nucleus of the teleutospore is heterotypic, and really initiates the gametophyte; but, since this is not a sufficiently definite point in the cycle, it is usual to consider the gametophyte to begin after the next division, i.e. by the formation of the four basidium cells, which constitute a tetrad. These four cells are the true tetraspores. In water, deprived of air, they can each send out a germ-tube and, it is presumable, could cause infection. The formation of basidiospores on sterigmata is a secondary process, viz. the production of conidia suitable for wind-dispersion: this is shown by the fact that, if the basidiospores are not on the proper host plant, they can themselves germinate with the production of fresh conidia of an exactly similar character.

The mycelium (thallus) of the *gametophyte*, issuing from the basidiospores, bears male and female organs, the spermatogones and æcidia. The spermatia disintegrate without any result: the "fertile" cells of the æcidium (usually, perhaps nearly always, after cutting off a sterile cell, as is the habit of female gametes) are stimulated to further growth by conjugation with one another, the delay in the fusion of the nuclei being of little or no importance from this point of view. This so-formed fusion-cell is a zygote and is the beginning of the *sporophyte*. The æcidiospores and uredospores which are borne by this are conidial forms, devoted to increased multiplication, and may continue indefinitely till the time arises for beginning the cycle again. This is indicated by the dotted lines on the left of the diagram.

It is known that a fusion of two nuclei, comparable with that

which takes place in the maturing teleutospore, occurs also in the basidium of the Agaricini and Polyporei, followed by a division of the fusion-nucleus into four nuclei of which one passes into each basidiospore, although it is not yet ascertained how or where the cells of the hyphae of those Fungi become binucleate. From this point of view it is evident that the chief difference between the basidiospore-formation in the Basidiomycetes and in the Uredinales lies in the fact that, in the former, the four tetraspore-nuclei are not surrounded by cell-walls previously to the production of conidia, as they are in the latter.

The basidium of some of the Hemibasidiomycetes, e.g. of the Auriculariae, is divided into a row of four super-imposed cells of an exactly similar character to that of *Puccinia*, each cell also giving rise to a basidiospore on a sterigma in the same way. The similarity of this basidium to that of *Coleosporium* is not diminished by the fact that it also is surrounded by a gelatinous mass through which the sterigmata protrude. Had not this primitive mode of forming the conidia been modified into that typical of the Agaricini, there would have been no opportunity for those wonderful and intricate contrivances for facilitating spore-dispersal which Buller has pointed out (1909) and which find their highest and latest development in *Coprinus*.

The Uredinales must be considered a highly organised group of comparatively recent evolution, as is evident also from their exceedingly complex parasitism. They are not a stage in the evolution of the ordinary Basidiomycetes, but the end-group of a different branch.

NOTE. Werth und Ludwigs (1912) showed that the teleutospores of *Puccinia Malvacearum* arise by the conjugation of two basal cells like those of an æcidium, but usually of unequal size. The nucleus of the smaller cell passes into the larger; the fertilised cell then forms, by conjugate division, a short chain of binucleate cells, of which the two upper become the teleutospore.

CHAPTER III

SPORE FORMS OF THE UREDINALES

ÆCIDIUM.

Æcidia are usually of a cup-like shape, partly embedded in the host, and with the free protruding edge more or less recurved. This is the typical and presumably the most highly evolved form. In it the spores are at first completely enclosed by a firm structure, the *peridium*, the cells of which have the membrane thickened on the inside wall or the outside or both, and are arranged in very definite rows like the spores. But there are a number of variations on this type, most, if not all, of which belong to a lower stage of evolution. Sometimes the peridium has the cells less definitely arranged in rows, and therefore opening more irregularly; at other times the peridium is thin-walled and delicate, and in that case it usually opens by a rounded pore and the edges do not roll back. In *Hyalopsora* and its allies such a peridium is formed round the uredo-sori, and there are reasons for believing that in these cases the pore arises just beneath a stoma. A still simpler stage is represented by those cases where there is no definite peridium at all, but merely a surrounding circle of paraphyses which in a few cases are almost or even totally non-existent. This is called a Cæoma and indicates a more primitive form; it is found in *Phragmidium* and *Melampsora*. In the non-British *Gymnoconia Peckiana* (= *Puccinia Peckiana*, on *Rubus*) peridium and paraphyses are both entirely absent.

Again, if there is a definite peridium, it need not have the shape of a cup. It may be elongated-cylindrical, straight or curved like a horn: this is called a Roestelia and is confined to

the genus *Gymnosporangium*, on the Pomaceæ. Or it may be oblong or globular, and more or less inflated: this is called a Peridermium, and appears to be confined to the Coniferæ (leaves and stems) as hosts and to belong only to the genera allied to *Coleosporium* and *Cronartium*. None of the Peridermia have been found in Australia. It is a remarkable fact that æcidia are never found upon Juncaceæ and Cyperaceæ, nor upon Gramineæ with only two exceptions—the æcidium of *Uromyces Danthoniæ*, on *Danthonia* in Australia, and of *Puccinia graminella*, on *Stipa* in North and South America. In all other Uredines parasitic on these families, if æcidia enter into the life-cycle of the fungus at all, they are formed upon some broad- and thin-leaved Monocotyledon, or upon a Dicotyledon, usually though not invariably belonging to one of the more specialised orders and above all to the Compositæ.

The essential characteristic of the æcidium is that its spores are produced in chains from a fusion-cell, as described in Chapter I. The spores themselves are always unicellular, mostly with orange contents, and separated by intercalary cells. Their customary polygonal shape arises entirely from crowding and their verruculose sculpture presents a remarkable similarity through all the group. The cells of the peridium of the higher types are homologous with the æcidiospore-mother-cells, and represent a division of labour for the sake of protection: the paraphyses and the lower forms of peridium are not of the same character, and may have had a somewhat different origin. All æcidiospores, except those of *Endophyllum*, germinate conidially as in *P. Caricis* and the germ-tubes enter the host through a stoma: the germ-pores are numerous and almost always indistinct.

When there are secondary æcidiospores, i.e. such as arise from the germination of a previous æcidiospore, they always take the place of uredospores. In such cases, only the primary æcidiospores arise from fusion-cells, and are accompanied by spermogones. There is said to be one case where æcidiospores are uninucleate, and thus comparable with azygospores, but further evidence is required before this statement can be accepted (Moreau, 1911).

SPERMOGONES.

While æcidia are always subepidermal, and in the higher forms sunk rather deeply in the tissues of the host, the spermogones are in certain genera subcuticular and in others subepidermal, but always shallow. This doubtless corresponds to the primitive form of the æcidium, when the trichogynes protruded through a stoma in order to catch the spermatia. When fertilisation was dropped, it became possible for the æcidia to be surrounded for protective purposes by a continuous and firm peridium and to be more deeply sunk within the host: the spermogones, being outside the range of selective evolution on account of their uselessness, have retained more or less of their original character. The description of those of *P. Caricis* applies essentially to nearly all, except that in certain genera they are flat, not flask-shaped, and open by a wide pore, not by an ostiole, and in these and others there are no protruding filaments.

Spermogones never appear alone; they are always accompanied or closely followed by some other spore-form, either æcidio-, uredo-, or teleutospores. In comparatively few cases, as in *P. Malvacearum*, have the spermogones disappeared entirely.

UREDOSPORES.

Uredospores are usually distinguished from æcidiospores by being produced singly at the apex of a short pedicel from which they easily fall off: this pedicel is the homologue of the intercalary cell of the æcidiospores, as was shown by Christman. In certain genera, however, e.g. *Coleosporium* and *Chrysomyxa*, the uredospores are produced in short chains. Uredospores can reproduce uredospores for an indefinite number of generations. Occasionally there are two kinds, primary and secondary uredospores; in such cases the primary ones arise from fusion-cells and take the place of æcidiospores. So far as is known true uredospores never arise from a uninucleate mycelium, though they may spring from a mycelium which was at first uninucleate, but became binucleate at some point in its development.

This would be the case in a true Hemipuccinia, but none of these have so far been cytologically investigated.

Uredospores are always unicellular, except in the case of a few monstrosities. Primarily they must be considered a device to aid in rapid propagation and hence may be called *summer-spores*: for this reason they usually germinate with great readiness when mature, always forming a tube which enters a stoma of the host. The number of germ-pores varies from 1 to 10 (usually 2 to 4): only one case is known in *Uromyces* where they possess a single pore (*U. uniporus*) and one in *Puccinia* (*P. monopora*). They present a wonderful sameness in shape throughout the whole group, and in colour vary from yellow and orange to brown. It may be taken as a general rule that if the wall is colourless, the contents are yellow or orange from an abundance of that yellow oily substance which occurs in æcidiospores; if the wall is distinctly brown, the contents are often colourless when mature, though at first they frequently contain the usual yellow oil. It is only in a few instances, in the lowest genera, that uredospores are quite without colour. The uredospores of *Puccinia dispersa* and in a smaller degree of *P. graminis* are noticeable for a curiously dull appearance which is very characteristic, because they combine orange contents with a brownish membrane. The outer wall of uredospores is almost always covered with spines (echinulate), needles (aculeate) or warts (verruculose); it is very rarely smooth; these projections enable them to cling more readily to the surface of the host. They are often intermixed with paraphyses, which are usually clavate or capitate in shape; these are found in a few species of *Puccinia*, but more especially in *Melampsora* and *Phragmidium*. These paraphyses are homologous with the spores, being binucleate at first, but the nuclei soon disintegrate.

There is very frequently found in the uredo-sori of many species a parasite belonging to the Deuteromycetes, called *Darluka Filum*. It consists of a black pycnidium, enclosing numerous uniseptate pycnosporcs which are faintly apiculate at each end. This has been sometimes mistaken for another spore form of the Uredine.

AMPHISPORES.

In countries which are arid or semi-arid, there is found in certain species a form of uredospore which has led to several mistakes owing to its misleading appearance. The spores are provided with a thick cell-wall or have the summit thickened conically, after the style of many a teleutospore of *Uromyces*, and are supported on a persistent pedicel, so that one would not take them for uredospores: nevertheless they will be found to have more than one germ-pore and to germinate by a germ-tube, although only after a period of rest. These were named by Carleton *amphispores*: they were first discovered in *Puccinia vexans*. They are evidently a provision to enable the spore to pass through an unfavourable period unharmed, and reinfect a host of the same species when occasion arises. The amphispores of *Puccinia atrofusca* Holway, though echinulate and possessing two equatorial germ-pores, were first described by the discoverers, Dudley and Thompson, as the teleutospores of a *Uromyces*, and the same thing has happened in other cases, e.g. *Puccinia convolvuli*, *P. tosta*, and *P. cryptandri*. The



Fig. 22. Amphispore of *Puccinia Pruni-spinosae*. $\times 600$.

nearest approach to amphispores found in British species is in *P. Pruni-spinosae* (Fig. 22), in which they have been mistaken for paraphyses and were so figured in a well-known text-book. There is another kind of spore, presently to be described, called a *mesospore*, which bears a superficial resemblance to an amphispore. It is a mistake to call amphispores a transition-form between uredo- and teleutospores, since they are of later evolution than the two latter.

TELEUTOSPORES.

The meaning of the word teleutospore is *end-spore*; it was considered to represent the stage when growth was ceasing for the season. This is not the case, however, in all species, and the word must now be used with another connotation, viz. a teleutospore is one which germinates by the production of a basidium and basidiospores.

The teleutospores are generally produced in sori like those of the uredospores; they frequently arise on the same mycelium, and very often on the same spore-bed, mingled with the uredospores. If both are found in any species, the teleutospores are always formed at least not earlier, and usually later than the uredospores. Their primary function now is to tide over an unfavourable period; for this reason they are sometimes called, in England, *winter-spores*. They may be one-celled as in



Fig. 23. Figures of various Teleutospores of Pucciniaceæ (after Sydow). From left to right, they are (in the top row) *Puccinia roesteliiformis*, *P. conspersa*, *P. globosipes*, *P. Megatherium*, *Uromyces globosus*, *Hapalophragmium Derridis*; (in the second row) *P. appendiculata*, *P. Euphorbiae* var. *intumescens*, *P. deformata*, *U. achrous*, *U. giganteus*, *U. Ipomoeae*, *Triphragmium Cedrelae*. All $\times 480$. (Non-British.)

Uromyces, two-celled as in *Puccinia*, radiately three-celled as in *Triphragmium*, cruciately four-celled as in *Pucciniastrum*, linearly many-celled as in *Phragmidium* and especially in *Xenodochus* (see also Fig. 23). But it is misleading to speak of a many-celled spore: each cell, taken separately, is a spore and can germinate by itself without reference to the others.

In the formation of teleutospores in the higher Uredinales, the spore-mother-cell first divides into an upper fertile cell and a lower sterile cell, which elongates more or less to form the pedicel. The upper cell may remain undivided, or may divide again: the lower of these two may then continue to divide and so on, to form a many-celled chain. When the chain is long, as in *Xenodochus*, it is seen very clearly that the spores are formed like aecidiospores to this extent that the uppermost is always the most mature. This may be taken as a sign that they are modifications of aecidiospores to form resting-spores. In *Endo-phyllum* the aecidiospores previously mentioned germinate as soon as mature with a basidium, and are therefore teleutospores also: this is the primitive state of things from which the present wide division of labour into rejuvenating (aecidio-), multiplying (uredo-), and resting (teleuto-) spores has been evolved.

In some of the lower Uredinales, the teleutospores are formed beneath the cuticle or in the epidermal cells, but the usual position is directly beneath the epidermis. Throughout the whole group the colour of teleutospores is almost uniformly brown, varying in shade from a pale yellowish-brown up to nearly black. Their contents are, like those of uredospores, at first often oily and yellow, afterwards colourless. In the lowest genera, those found on Ferns, the teleutospores are quite hyaline.

Their surface is most often smooth externally, but occasionally marked with superficial unevennesses, such as warts, tubercles, lines, striae, reticulations, and pits; a few have spiny, papillose, or finger-like processes, either at the summit or all round. The majority of them have one pore to each cell, as in *Puccinia* and *Uromyces*, covered at times by a distinct, often hyaline, pore-cap; this is the highest type, being furthest removed from the many-pored aecidiospores. Other genera have 2 to 4 germ-pores to each cell, as in *Phragmidium* and *Gymnosporangium*. In some cases, as in *Uromycladium* and *Ravenelia*, the teleutospores are borne in bunches at the top of a common stalk, either with or without accompanying hyaline cysts, i.e. abortive spores. An approach to this is found in the

British *Puccinia Pruni-spinosae* and other species, where the short pedicels are all closely bound together in bunches at the base. Paraphyses are naturally not so common in teleuto-sori as with uredospores, since the former do not need such protection, but they are found in *P. Sonchi*, *P. dispersa*, *P. persistens*, etc., although in these cases the so-called paraphyses are not at all of the same character as those found in uredo-sori, e.g. of *Puccinia Baryi* and others. When the teleutospore of a normally two-celled species becomes one-celled (by the omission of the last cell-division), it is called a mesospore: the mesospores of *Puccinia* are practically identical with the teleutospores of *Uromyces* and germinate like them.

BASIDIOSPORES.

All normal teleutospores develop under natural conditions in the same way; the cell-contents divide themselves into four parts, by a heterotype followed immediately by a homotype mitosis.

This formation of what are really (and might with advantage be called) *tetraspores* can take place in two ways:—the “basidium” can arise within the teleutospore-cell or outside it. The first method is the more primitive, the second is an adaptation to the tough cutinised or chitinous exospore of the more advanced types. In the *Coleosporiaceæ* the teleutospore, i.e. the tetraspore-mother-cell, divides into four superposed cells (like the tetraspores of *Corallina*) while still in the sorus, during the autumn; each cell (spore) germinates, in late autumn, by protruding a sterigma through the thin gelatinous wall of the teleutospore and forming a basidiospore (conidium) at its apex. *Zaghouania* shows an intermediate form of germination. But in all the other families the cell-contents of the teleutospore, clothed only in a thin endospore, pass out through a germ-pore in the form of a longer or shorter tube (“basidium”); the contents pass to the distal end of this, and are there divided into four oblong cells. The median septum is sometimes formed first, and the two lateral ones after. In water the “basidium” is usually long, in air it is short. In the absence of sufficient

air, moreover, the four cells may not be formed: the "basidium" may resemble, more or less, an ordinary germ-tube and possibly may function as such. Even if the four cells are formed, they may germinate by the protrusion of a germ-tube, which presumably can cause infection by penetrating the cuticle (see Coons, 1912, p. 225). But, with access of air, each cell forms a sterigma and a basidiospore as previously described. These conidia are obviously adapted for wind-dispersion. If they alight on a suitable surface, they send forth a short tube which invariably bores straight through the cuticle into the underlying epidermal cell of the plant, and there begins to form a mycelium. The only instance in *Puccinia* known to the contrary¹, out of the many observations that have been made and figured of this process, is De Bary's record of the case (*Ann. Sci. Nat. Bot.* 4, xx, 1863, pp. 88-9) where the germ-tubes of the



Fig. 24. Basidiospores (*b*) of *Puccinia Dianthi*, germinating on leaf of *Dianthus*, showing the germ-tubes making straight for the stomata (after De Bary's figure). $\times 390$.

basidiospores of *Puccinia Dianthi* (q.v.) penetrated through the stomatal openings of *Dianthus barbatus* (Fig. 24). In grasses and sedges, it is easy to see that the siliceous cuticle would present a great obstacle to the entry of such a tube, while not impeding germ-tubes which enter through a stoma, and this is probably the reason why

æcidia are so rare on the order Glumifloræ. In the heterœcious species no one has yet brought forward indisputable evidence to show that basidiospores can infect the host which bore the teleutospores, although statements to that effect are made.

The shapes of basidiospores are not irregular; they are more or less constant in each group. In *Puccinia* and *Uromyces* they are ovate, somewhat flattened on one side, or kidney-shaped. In the Phragmidieæ they are almost spherical; in the Melampsoraceæ small and roundish. In *Endophyllum* they are ovate; in *Coleosporium* they are large and ovate and a

¹ Statements have been made of other instances, but most of them on insufficient authority, and some have been specifically disproved. The genus *Coleosporium* seems, however, to be an exception.

little flattened on one side, while in *Ochropsora* they are spindle-shaped. This is one of the reasons for suspecting that it is probably incorrect to classify these two latter genera in the same family, on the basis of the "internal" basidium merely. The genus *Chrysopsora*, which has the same kind of basidium, belongs to the Pucciniaceæ.

GROUPING ACCORDING TO SPORE-FORMS.

For certain purposes it is convenient to have names for the groups into which the Uredinales may be divided according to the number of spore-forms possessed by each, though it must never be forgotten that such a grouping does not in any way indicate affinity. The method usually employed is that put forward by Schröter, which (with a little modification according to present ideas) may be presented in the following scheme.

Denoting spermatogones by O, æcidia by I, uredospores by II, and teleutospores (with the ensuing basidiospores) by III, we call a fungus possessing

O I II III	a Eu-form	{ Auteu-form, if with all four on one plant. Hetereu-form, if O, I on one species, and II, III on another.
O I III	an -opsis-form.	
O II III	a Brachy-form.	
II III	a Hemi-form (in many cases perhaps the half of a Hetereu-form).	
[O] III	a Micro-form (spermatogones sometimes absent).	

Thus *Melampsora Rostrupii* is a Eumelampsora, *Gymnosporangium Sabinæ* is a Gymnosporangiopsis, *Uromyces Anthyllidis* is a Hemiuromyces, and *Puccinia Campanulæ* is a Micro-puccinia. A Leptoform is one, of whatever kind, in which the teleutospores germinate as soon as mature, without any resting period; thus the spores of *P. Malvacearum* belong chiefly to the lepto-form, those of *Endophyllum Sempervivi* entirely so.

Maire (*Progress. Rei Botan.* 1911, iv, 115) has proposed a much more complex arrangement on the same lines, which is quite needless and, it is to be hoped, will be quietly ignored.

The relations of the various groups to one another are represented in the following diagram. The curve represents the Eu-forms; the substitution of any one chord in the place of the arc which it subtends shows how the life-history is shortened in the other cases. Only the abnormal *Ectodophrum* cannot be included in such a scheme; its spore-grouping could only be represented by the symbol $O \begin{smallmatrix} I \\ III \end{smallmatrix}$.



CHAPTER IV

LIFE-HISTORIES OF OTHER UREDINALES

Puccinia graminis.

THE BLACK RUST OR "MILDEW" OF CORN.

Another common *Puccinia*, whose life-history is of greater economic importance than that of *P. Caricis*, is the well known *P. graminis*, the Rust or Mildew of Corn. This species has its spermogones and æcidia on Barberry (*Berberis vulgaris* and *Mahonia Aquifolium*) and its uredo- and teleutospores on many species of grasses, especially on cultivated wheat. It must not, however, be assumed that any rust found on wheat is *P. graminis*; there are at least two other species common on the same host which, unless carefully examined, may be confounded with it, viz. *P. triticina* and *P. glumarum*, not to mention a form of *P. coronata* which sometimes also occurs on cereals. For this reason these four species are now distinguished as the Black Rust, Brown or Orange Rust, Yellow Rust, and Crown Rust of corn, respectively. The uredo-stage of *P. graminis* is known as Red Rust.

If one merely substitutes Barberry for Nettle and Wheat for *Carex*, what has been said about *P. Caricis* is true in all essentials of *P. graminis*. The differences are not in the life-history, but in certain minor details of occurrence: e.g. the spots caused on the leaves of Barberry are small, round and red, while uredospores of *P. graminis* are most common on the leaves, and the teleutospores form long black striæ on the

culms: for these differences the systematic part can be consulted (Fig. 25).

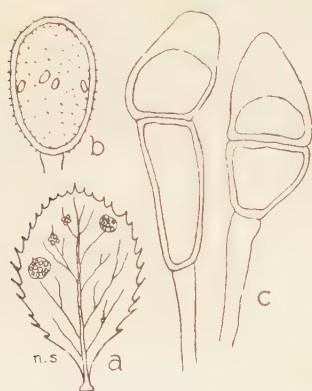


Fig. 25. *Puccinia graminis*. a, aecidia on *Berberis*; b, uredospore; c, teleutospores.

There is, however, one point of difference connected with *P. graminis* which possesses great biological interest—its virtual independence of the aecidial stage. For a long time it had been known that Barberry bushes in the hedges caused “mildew” on the corn in the neighbouring fields, and when, in 1864–5, De Bary proved the heteroecism by experimental cultures, it was too hastily assumed that the aecidium on the *Berberis* was just as essential to the rust on the corn as

that on the Nettle is to the rust on the Sedge. Many facts now tend to show that this is not the case.

In Australia and the plains of India the Barberry is unknown except as an introduced plant, yet the *Puccinia* occurs everywhere and does enormous damage. McAlpine records, in his *Rusts of Australia* that he made numerous attempts to infect imported species of *Berberis* with the rust of Australian wheat which is morphologically undistinguishable from the *P. graminis* of Europe, but all his efforts were in vain. The inevitable inference is that *P. graminis*, as it occurs in those countries, is a “biological” race which maintains itself by other than the primitive means. A similar thing is true, according to Lagerheim, in Ecuador, where also rust flourishes and does great harm.

The facts now known concerning the specialisation of the Black Rust are treated of in a separate chapter, but there is one point which must be mentioned here. This concerns the mode by which fresh epidemics are produced each year. Even if the Barberry is present, it is by no means certain that it plays any important part in these annual attacks. Apart from that, there are several possibilities: (1) the fungus may winter

by its uredospores, (2) by a perennial mycelium, (3) by Eriks-son's mycoplasma.

The first possibility is entirely a matter of climate: it may take place in one country and not in another, or in the same country it may take place in one season and not in others. McAlpine and Cobb find viable uredospores all the year round in Australia, and Lagerheim says the same for Ecuador. But in northern climates it has been shown that the uredospores of *P. graminis* frequently lose all capacity for germination during the winter; this is proved true of Sweden, North Germany, North Dakota, etc., but in the United States, south of Ohio, Bolley found germinable uredospores all through the year. Similarly in Bohemia, uredospores of *P. dispersa*, *P. glumarum* and *P. Lolii* can survive mild winters or in sheltered places (Baudys). Even though uredospores capable of germination may sometimes be found on wild grasses during the winter, it does not follow that those could start an epidemic next spring, owing to the specialisation which has been proved to exist, by which a form of *P. graminis* on one host is often incapable of infecting another host.

In regard to the second possibility, we find again two opposing views. De Bary and others have searched in vain for mycelium in the growing wheat plants, before infection becomes visible, but Pritchard (1911) found mycelium resembling that of *P. graminis* both in the pericarp of wheat grains and in various parts of wheat seedlings. He showed that large numbers of wheat grains contained pustules of teleutospores, even visible in the neighbourhood of the hilum, but also hidden within the pericarp. He proved that the mycelium from the pericarp penetrates through the intercellular spaces, as well as through the cells, and "soon passes into the spaces between the leaf-sheaths where it grows rapidly and attacks the tissues at various points." W. G. Smith figures teleutospores within the seed of Oat (*Gard. Chron.* 1885, xxiv, 245, f. 53) and æcidia in the pericarp and seed of Barberry (*ibid.* 1886, xxv, 309, f. 58).

It is evident that, if this state of things prevailed on a large scale, nothing more would be required to explain the

origin of outbreaks of rust. It is not inconsistent with this that Ward was able to prove that the mycelium of a uredosorus extends only a little way round the margin of the sorus: that may be and is true in certain cases, especially with regard to secondary uredo-sori, but in *P. Curicis* the mycelium extends up and down the leaf between the parallel vascular bundles, producing uredo-sori all along its course. The practical bearing of Pritchard's discovery is to show that seed from an infected crop should never be used for planting.

About the third possibility, it is difficult to come to any definite conclusion. Eriksson's hypothesis is that the protoplasm of the fungus is present in the grain, mixed with the protoplasm of the host, in such a way that the two are indistinguishable. As the plant grows up, he supposes that the two grow together until, at a certain time, the protoplasm of the fungus separates itself from that of its host in the form of "Nucleoli," passes into the intercellular spaces through "invisible pores," then or earlier surrounds itself with a cell-wall, forms a mycelium, and begins its ordinary life by producing uredo-pustules. An intermediate stage, where the fungus-protoplasm has surrounded itself by a cell-wall but is still enclosed within the cells of its host, he named "special corpuscles."

The difficulty in dealing with this theory lies in its indefiniteness; its author changes it from time to time to meet objections, and supports it by hazy microscopical observations, many of which are demonstrably the result of incorrect vision. His "special corpuscles" have been shown by Ward and Klebahn to be ordinary haustoria. Eriksson having completely overlooked the intercellular hyphæ to which those haustoria were attached. It is incredible that the protoplasm of so highly evolved a fungus could live outside its cell-walls, as he supposes. Such a state of things is, of course, common in the lower fungi, Chytridinae and allied groups. In *Synchytrium Solani* the fungus-protoplasm and the host-protoplasm may be seen in the same cell, before the latter has been completely devoured by the former, and in that state they are even distinguishable by their microscopic appearance. But it will need a great deal more "proof" before

Eriksson's startling hypothesis can be accepted in regard to such a fungi as the Uredinales.

The futility of Eriksson's mode of argument is seen in his suggestion (1908) that "other diseases such as the American Gooseberry Mildew can live within the infected shoots *in a form scarcely visible to our eyes.*" But direct evidence against the Mycoplasma Theory is accumulating. Jaczewski (1910) grew seeds obtained from many much-rusted plants, but he found that, when they were sown under glass and protected with *adequate* care from all outside infection, they *all* produced rust-free plants. Bolley, Linhart, Zukal and Klebahn had similar experiences¹. Zach (1910) on investigating leaves and culms of Rye, infected with *P. graminis* and *P. glumarum*, found on the outskirts of the infection-patches all the states described by Eriksson, but he proved that in all of them fungal hyphæ were present. In fact, Eriksson himself saw and represented these hyphæ, but calls them "radialen Stränge" of his supposititious "Nucleoli," the said "Nucleoli" being merely the deformed remains of the nucleus of the attacked cell. As Marshall Ward (1905) remarked, Eriksson merely *inverts* all the stages of a fungus attack on a cell, and supposes the last state to be the first. This error and a misinterpretation of the microscopic appearances account for the whole wearisome persistence in an inherently improbable hypothesis.

Puccinia Poarum.

THE COLTSFOOT AND MEADOW GRASS RUST.

This species is economically of no importance; its spermo-gones and æcidia occur on the common Coltsfoot (*Tussilago Farfara*), and its uredo- and teleutospore stages on species of *Poa*, to which however they do little harm. Here, again, the

¹ This does not accord with Eriksson's experience; but then on some of his "protected" plants aphides also made their appearance, yet this does not seem to have suggested to him that the *zooplasm* of the aphides must also have been latent in the seed! If the aphides got in, so would fungus spores, since it has been proved (Butler, 1905) that uredospores are carried by them and other insects.

life-history is in all essentials identical with that of *P. Caricis*, but it differs in one striking particular—there are two generations of each stage during the year.

The spermatogones and aecidia first appear on the leaves of Coltsfoot in May and June, and are followed by the *Puccinia* on neighbouring leaves of *Poa* in July and August. Then a second crop of aecidia, also accompanied by spermatogones, appears from end of July to September, followed again by uredo- and teleutospores in September to November. The latter rest during the winter and infect the young Coltsfoot leaves again in the following spring. In countries that have a climate favourable for the growth of *Poa*, the uredospores may be found the whole year round, and the fungus can maintain itself by them alone. This is certainly the case in Australia, according to McAlpine, where the Coltsfoot does not exist, and the uredo-stage is most common in the winter months, i.e. June to September. In this country, the teleuto-sori are rather inconspicuous, but can be found by searching carefully on the lower leaves of species of *Poa* round the spot where the Coltsfoot has been found affected by the æcidium, especially in July and August.

The æcidium of this species has been examined cytologically by Blackman and Fraser, and according to them the binucleate condition of the fertile cells is produced by the migration of the nucleus from one fertile cell to an adjoining one in the hymenial layer, and also occasionally by a migration from one vegetative cell to another at a point where the conjugating cells were below the level of the hymenium, although only a little lower. Cells with three or four nuclei were met with by them, and true conjugate division was observed in such cases.

In sections which I have examined of this species, I have seen evidence which seemed to indicate (although not with perfect certainty) that conjugation also took place by the removal of a large part of the intervening cell-wall, and a consequent fusion of the cells as described by Christman and Dittschlag (Fig. 26).

As will be seen from the figure, the cells of the peridium of this species differ slightly from those of *P. Caricis* in their shape.

as shown in radial section. The outer edge of each cell is more prolonged downwards so as to overlap a portion of the cell below in an imbricated manner. The æcidium, in both, as is the

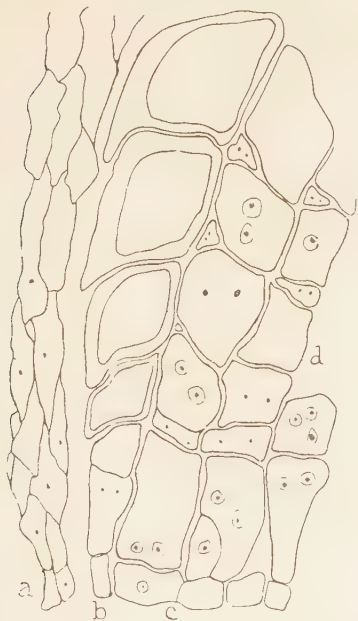


Fig. 26. *P. Poarum*. Vertical section through edge of æcidium; showing *a*, the crushed cells of the upper mycelium, pushed on one side; *b*, the chain of peridium-cells; *c*, the spore bed, giving rise to *d*, the chains of æcidiospores. $\times 600$. The black dots are the nucleoli; one æcidiospore-mother-cell has three nuclei.

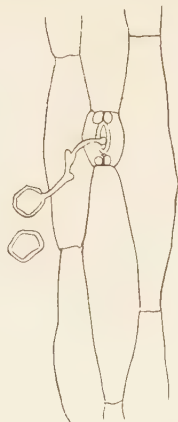


Fig. 27. *P. Poarum*. An æcidiospore germinating on leaf of *Poa annua*. $\times 180$.



Fig. 28. *P. Poarum*. *a*, an æcidiospore germinating in water, $\times 250$; *b*, the same, showing the germ-pores, $\times 500$.

case in most of the higher forms of the Uredinales, arises deep in the leaf, and the densely packed knot of hyphæ which forms the starting-point of the hymenium, where the cells are full of protoplasm, is covered over by a number of nearly empty cells which are ultimately squeezed to the side by the developing æcidium and are shown in the figure at *a*.

It is easy to produce the teleutospores in a garden on a tuft of (say) *Poa annua* or *P. pratensis*, by planting quite near to it

and overhanging it some Coltsfoot affected by the æcidium: another tuft about ten yards off can be used as a control. The uredo- and teleutospores will appear on the former tuft in about 14 to 21 days. If this is done late in the year (September) I have found that only teleutospores are formed on the leaves of the *Poa*. For the germinating æcidiospores see Figs. 27, 28.

Puccinia Malvacearum.

THE HOLLYHOCK RUST.

This Rust differs from all the others that will be mentioned in the simplicity of its life-history, and also in the fact that it is not confined (as almost all the others are) to one kind of

plant or even to a few, but appears, so far as is known at present, to range over the greater part of a sub-family. It has been found on over 50 species belonging to nearly all the genera of the Malvæ, and it seems to be identically the same in every case.

The mycelium develops in spring in the intercellular spaces of the young leaves and stems and produces little knots under the epidermis, on which a thick, round, hard, pale-reddish cushion of teleutospores is formed. These spores have short or very long pedicels according to their position; they are mostly typical and two-celled, but mesospores with only one cell are not uncommon, and occasionally a few may be met with having three or even four cells. Most of them germinate at once, in the sorus, producing basidiospores in the usual



Fig. 29. *P. Malvacearum*. Germinating spore; a, a basidium breaking up into separate cells; b, a basidiospore, $\times 600$.

way (Fig. 29). The accumulated basidia and spores give a greyish tinge to the red-brown sorus. These spores can cause fresh infection and so the disease spreads rapidly. It is most active about the end of summer, and has often been the cause of a serious epidemic on the more susceptible kinds of Hollyhock. The sori are found on every green part of the plant, stems, leaves, petioles, bracts, sepals, carpels and fruits, and are even reported on the petals. There are no uredospores.

The chief biological interest of this fungus concerns the way in which it passes the winter, a point about which there has been much dispute. There are two possibilities, (1) by perennial mycelium, (2) by over-wintering teleutospores. The first has been strongly advocated, and it is very likely (though one can hardly say it has been proved) that the mycelium does winter in the young leaf-rudiments that are formed on shoots at the base of last year's stems. Freshly formed sori have also been found on the cotyledons of seedlings which grow up in late autumn round the parent plants and which in certain cases can survive the dead season. But there seems to be absolutely no justification for the claim that the mycelium winters in the embryo of the seed. The disease can undoubtedly be carried *with* the seed, in sori either on the bracts (portions of which are often mixed with the "seeds," i.e. fruits) or on the outside of the carpels themselves.

Eriksson has lately (*Ueber den Malvenrost*, 1911) published a theory, similar to his well-known theory about the Rust of Corn, and standing or falling with it: he says that *P. Malvacearum* perennates in the form of "mycoplasma" in the cells of the autumn buds at the base of the shoots, as well as in the embryos of the seeds of the infected plants. With these he says it grows up in an imperceptible form, mingled with the protoplasm of the host, permeating the newly-formed leaves and at last suddenly breaking out in the form of pustules of primary teleutospores, which afterwards spread in the acknowledged way. He explains the presence of this mycoplasma by stating that certain teleutospores of the previous autumn germinated by sending out "germ-tubes" which cut off "end-conidia." (This mode of germination of the late-formed spores

of *P. Malvacearum* is well known, though not usually interpreted in that way, see Fig. 29.) These "end-conidia" do not form a short tube, to penetrate the cuticle of the host, but "pour forth their protoplasm, as it seems, without the formation of an opening, through the plasma-connections of the outer wall of the epidermis of the host into an epidermal cell," and so into the tissues where it vegetates till required. It also exists in the same state in the seeds of the infected plants. The fungus, he says, "passes from the plasmatic into the filamentous state just before the outbreak of the primary pustules." It is clear, however, that the figures he gives do not prove what he asserts.

Putting aside this purely supposititious and intangible method, the chief means of perennation probably lies in the fact that certain teleutospores produced at the end of the growing season have the power of lasting through the winter and germinating in the spring. Plowright, Massee and Taubenhaus all agree in this: the latter (1911) kept infected leaves, gathered at Cornell University in the United States from the living plant on November 26th, both indoors at a low temperature and outdoors, and by testing spores taken from them at intervals from December to April found that they still remained germinable, though more and more slowly as time went on.

Dandeno, however (9th Report Mich. Acad. Sci. 1907, p. 68), states that the fungus does not winter in the seeds; he tried seeds of diseased plants, carefully excluding infection from outside, and found that they all produced healthy plants. His experience also was that no teleutospores remained viable till the next spring, but that the fungus maintained itself the whole winter through on mallow plants in sheltered spots.

These differences may be partly a matter of climate, and as regards the "seeds," unless there were sori on them, they could hardly be supposed to carry the infection, even if they came from infected plants, except by the presence of "mycoplasma" or mycelium, neither of which has been proved.

For this reason the chief means of preventing the disease (apart from using "seed" from uninfected plants) must be to gather and burn all dead leaves from the infested bed. When

the disease does appear, spraying with Bordeaux mixture is the best remedy against its spreading. It is the very young shoots and the *upper* side of the leaves that most require spraying; although the pustules appear chiefly on the lower surface of the leaves, there can be little doubt that infection by the basidiospores takes place mainly through the upper surface.

Gymnosporangium clavariæforme.

THE HAWTHORN AND JUNIPER RUST.

This fungus produces its æcidia on the branches, leaves and fruit of the Hawthorn and on the leaves of the Pear, and its teleutospores (there are no uredospores) on branches of the common Juniper, where it causes fusiform swellings. There are three other allied British species, of which *G. Sabinae* also attacks the Pear, but its teleutospores are formed only on *Juniperus Sabina* (the Savin Juniper).

On the swollen branches of the Juniper, the parasite produces in April and May numerous orange masses, which ooze out and sometimes reach more than 1 cm. in height. They vary in shape, but are usually more or less conical or tongue-shaped (Fig. 30). They consist of a mucilaginous mass in which large numbers of teleutospores are embedded. The mucilage is produced by the gelatinisation of the cell-walls of the fungus, especially of the very long pedicels; it naturally swells and becomes more conspicuous in wet weather. The teleutospores germinate at once, while still in the mass; the basidiospores are produced in the usual way; it has been shown lately in another species (Coons, 1912) that they do not fall off, but are jerked off the



Fig. 30. *Gymnosporangium clavariæforme*. Masses of teleutospores on branch of *Juniperus communis* (slightly reduced); two teleutospores, $\times 600$.

sterigmata, much in the same way in which the basidiospores are thrown off in the Agaricini¹. They accumulate in large numbers on the outside of the mucilaginous mass, and present the appearance of a golden-yellow powder. The mycelium of the fungus is perennial in the Juniper, spreading from branch to branch and producing a fresh crop of teliospores each spring.

If one of the basidiospores is blown by the wind or carried by insects to a moist leaf or young fruit or stem of Hawthorn, it germinates and bores through the cuticle in the ordinary way, and forms there a limited patch of mycelium. It is said that the infection has been known to be conveyed for half



Fig. 31. *Gymnosporangium clavariæforme*. Æcidia on leaf, fruit, and branch of Hawthorn (reduced); a, peridium, $\times 16$. The fruit and gall on branch are shown as they appear when the peridia are old, and the mass looks somewhat like a honeycomb.

a mile. This mycelium produces the æcidium-stage, which is not usually seen until the end of June, in about 18—20 days. The æcidia are not of the ordinary cup-like shape, but of the form called *Ræstelia*: they are cylindrical, brown at the base and ochreous above where the peridium is torn into numerous slender filaments (Fig. 31). On the leaves they appear in roundish patches a few mm. in diameter, but on the twigs they form large spongy masses and the fruits are often so covered with them as to look like a cluster of little spikes.

¹ I am indebted to Professor Buller for calling my attention to this fact.

Within these æcidia the æcidiospores are produced; these will only infect the Juniper, on which they begin the cycle again.

For all these species of *Gymnosporangium* the only remedy is to remove and burn the diseased Juniper, if it can be found; if it may not be destroyed, at least the affected branches should be cut off, and the wounds dressed with Stockholm tar. It is of no use to spray or otherwise treat the Hawthorn or Pear. In them the disease is purely local; it comes to an end when the summer ends, and will not recur next year unless fresh infection is conveyed from the Juniper. The harm done to them is confined to the loss of the foliage which naturally weakens the tree to some extent.

Endophyllum Sempervivi.

THE HOUSELEEK RUST.

This parasite attacks the common Houseleek and numerous other species of *Sempervivum*. It differs from nearly all the other Uredinales in having only spermatia and æcidiospores, the latter functioning also as teleutospores and producing basidiospores. This fungus has been thoroughly investigated by Hoffmann (1911) from whom the following account has been derived.

The æcidiospores mature on the leaves in April and May; they have no visible germ-pores. They germinate at once, while still in the æcidium; the germ-tube forces its way out at some point of the circumference of the spore and elongates to form the four-celled basidium. Each basidium produces four basidiospores on long sterigmata; occasionally more are produced—Hoffmann observed as many as eight on one basidium. The basidiospores may be blown on to the leaf of a Houseleek where they germinate at once and bore through the cuticle; they form a holdfast (somewhat as a uredospore does) below the outer wall and penetrate into the epidermal cell (see Fig. 17). The mycelium then branches, passes through the intercellular

spaces (sending haustoria into the cells) until it reaches the base of the leaf; thence it penetrates into the axis and so up to the growing point, where it hibernates till the following year. In the spring it grows on into the freshly formed leaves which become yellow and longer and more erect: on these, on both sides, spermogones appear in March and April, followed



Fig. 32. *Aecidia* of *Endophyllum* on leaf of *Sempervivum montanum* (reduced).

by *aecidia* (Fig. 32) which repeat the cycle. The affected plants are easily recognised by the different attitude of the leaves, which imparts an unusual irregularity to the rosette (Fig. 33).

The most interesting point about this species is that established by Hoffmann, that the *aecidiospore-chain* arises in the way already described for *Puccinia Caricis* from a cell produced by the fusion of two adjacent cells of the spore-bed, after the manner described by Christman except that the conjugating cells were not situated in any definite plane. The binucleate *aecidiospores* then became uninucleate by the fusion

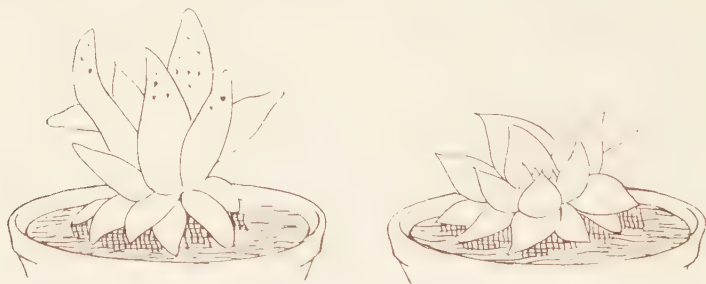
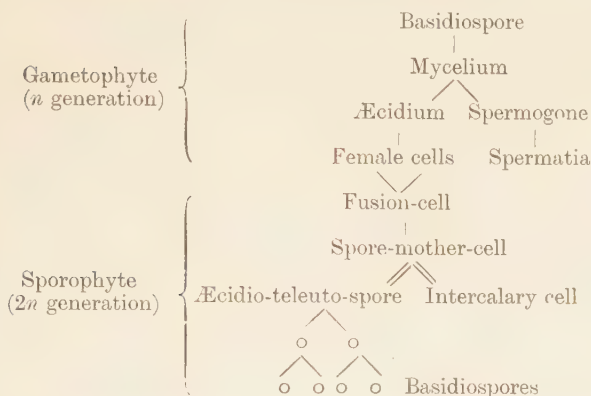


Fig. 33. Two plants of *Sempervivum*, one (left) affected by *Endophyllum Sempervivi*, the other not.

of the conjugate nuclei. On germination, when the fusion-nucleus divides into four, the first division shows slight differences from the others so as to make it certain that it is the reducing division.

The life-cycle may thus be represented as follows :



This life-history is especially worthy of consideration because it probably represents that which obtained at the first evolution of the higher Uredinales. The various types of development, seen in the genera *Puccinia*, *Uromyces*, etc., and described under the names Eupuccinia, Micropuccinia and so on, may all be derived from this original form. See Grove, *New Phytologist*, 1913, p. 89.

Cronartium ribicola.

THE RUST OF CURRANTS AND FIVE-LEAVED PINES.

This disease, called the Currant Rust in one stage, and the Weymouth Pine Blister Rust in the alternate stage, can do enormous damage in the second phase; it threatens in places to put a stop entirely to the cultivation of the Weymouth Pine. It has been imported into England and the United States with young trees of the latter from the continent of Europe. The remedy is to inspect Weymouth Pines, in nurseries and plantations, annually, cutting down and burning all those that show infection, and to remove all currant bushes from their neighbourhood. A currant-free belt, 300—500 ft. wide, is considered sufficient for security.

The teleutospores are produced on leaves of various kinds

of *Ribes* (Fig. 34); they have been recorded on 26 out of about 50 known species. The spermogones and æcidia are formed on stems and branches of the five-leaved species of *Pinus*: they have been found on five out of the eighteen Pines of that group, but do not attack species having 2 or 3 leaves in a fascicle. The following account is founded on that of Spaulding (1911).

The basidiospores are formed about the beginning of August, and if they are blown by the wind, and adhere to moist young branches of the Pine, the germ-tube enters and produces a mycelium which lives in the branch for several years, ultimately causing it to become considerably swollen in a fusiform or irregular manner. In about half the cases it is the main trunk



Fig. 34. *Cronartium ribicola*. a, a spore of *Peridermium Strobi*, $\times 600$; b, the teleutospore-columns on leaf of Red Currant (reduced); c, a uredospore; d, top of a column of teleutospores, $\times 600$.

that is infested. On this swollen portion spermogones appear at almost any period of the year, followed in spring by the æcidia, which break through fissures in the bark; these may be even as much as 1 cm. high, yellowish-white in colour, with orange spores. When the peridium bursts open, in an irregular manner, the spores may be carried by the wind to any plants of *Ribes* that may be near and can at once infect them. The distance to which the æcidiospores can be effectively carried is estimated to be less than 500 ft. These spores cannot infect the Pine; but if they fall upon a moist leaf of *Ribes*, the uredopustules usually appear, on the underside, in from 10 to 20 days.

These uredospores can, as usual, reproduce themselves on

any leaves of *Ribes* to which they may be carried, thereby forming a means of rapidly spreading an infection which is once started. After a few weeks, brownish thread-like growths appear in the uredo-sori: these are the filaments on which the teleutospores are borne, and the latter may be found from July until the fall of the leaf, and even upon the fallen leaves. The teleutospores may germinate at once, perhaps also after a considerable time, but the basidiospores which they produce can only infect young branches of Pine as described above. They are distributed by the wind, but probably cannot be carried to any great distance. Owing to the long incubation period of the mycelium which will produce the æcidiospores, the fungus cannot be seen on the Pine until it is at least three years old, although infection may have taken place in the seedling: by that time the leaves have naturally fallen off the part which received the infection.

Though this disease does little harm to the currant, it is necessary to destroy the infested bushes, since they form a focus of infection for the Pines. Weymouth Pines that are more than 20—25 years old are rarely liable to attack.

Melampsora pinitorqua.

THE PINE AND ASPEN RUST.

The æcidial stage of this *Melampsora* lives on young shoots of Scots Pine (*Pinus silvestris*) and its uredo- and teleuto-stages on leaves of Aspen (*Populus tremula*).

The teleutospores germinate after a winter's rest, and the basidiospores infect the young pine-buds, just beginning to elongate in May and June. The mycelium produced penetrates the cortex, and reaches also the bast and medullary rays. On these shoots the spermogones appear about the end of May, and are followed by the æcidia. The cortex of the affected part becomes orange and dead, while the unaffected part still continues to grow. Thus thin shoots may be killed altogether, but in the thicker ones curvature takes place owing to the one-sided growth: the negative geotropism of the growing

point, combined with this lateral curvature, causes S-shaped distortions which have given rise to the name "Pine Branch Twist" for the disease (Fig. 35).

It is suggested by Massee that the æcidiospores can reproduce the æcidia and thus propagate the parasite on the Pine without reference to the alternate host, but no proof is given of this statement. The mycelium is almost certainly perennial in the affected branch, and thus fresh outbreaks arise year by year more or less, according to the weather in the spring.

If the æcidiospores are blown on to a leaf of Aspen, they germinate there and the mycelium produces uredospores during



Fig. 35. *Melampsora pinitorqua* (from a German specimen, ex herb. Sydow). *a*, a young shoot of Pine, in June, with newly-formed leaves, showing three caomata (*æ*), shaded; the leaves have been removed from the affected portion, which is beginning to be curved; *b*, a caoma, $\times 10$; *c*, æcidiospores; *d*, old leaf of Aspen, showing numerous teleuto-sori on the lower surface; *e*, teleutospores.

the summer: these are usually so abundant as to cover the underside of the leaves, and the parts on which they occur show plainly as yellow spots on the upper side. For a time, the uredospores spread the disease rapidly during the growing season, until sometimes all the leaves of a tree are more or less attacked and are covered with a bright orange powder. As the leaves begin to die, teleuto-sori are formed; at first these are brown, and show as little angular crusts on the under side. Afterwards, when the leaves are fallen off, the crusts begin to turn almost black as the teleutospores mature. These spores are produced beneath the epidermis, standing erect and side by

side in crowded patches; they are brown and unicellular. They are not perfectly ripe till the following April; then, if the leaves are gathered from the forest-floor where they have lain all the winter, brought into a room and kept moist, the teleutospores will germinate in great numbers by sending out basidia in the usual way, though it is not possible to discern a germ-pore in the ungerminated spore. The basidiospores in turn infect the Pine, and the cycle begins again.

In the Aspen the mycelium affects only the leaves and causes little harm, since the leaves do not fall off prematurely: in the allied species, *Melampsora Rostrupii*, I have found the root-suckers round the parent tree to be most infested at first. Besides *P. tremula*, the Abele Poplar (*P. alba*) is also able to propagate the disease, as well as the hybrid between them, *P. alba* $\times$ *tremula*. The chief harm is done to the Pines: Hartig showed that seedling pines are often killed by an attack, but if the tree manages to survive over thirteen years it may recover. In any case the tree is more or less spoilt by the distorted and dead branches, and, if it is true that the acidiospores can spread the disease on the pines, it is evident that young seedlings, when seen to be infested, should be pulled up and burnt at once. Another precaution suggested by the life-history is not to allow plantations of the two species of poplar near to a seed-bed of Scots Pine.

It must be remembered that there are several other Uredinales on *Pinus silvestris*, and also others on the Aspen which have no connection with *Melampsora pinitorqua*: the latter species can be easily recognised by the curvature of the young pine-branches, which is not produced by any of the others. Fortunately the disease is rare in this country, as in many other countries.

Calyptospora Goeppertiana.

THE COWBERRY AND SILVER FIR RUST.

This fungus produces its teleutospores on the Cowberry (*Vaccinium Vitis-idaea*), and its acidiospores chiefly on the Silver Fir (*Abies pectinata*): it has no uredospores.

It can live at any rate for a number of years in the Cowberry, in which the mycelium is perennial, but in the Fir the mycelium is short-lived and perishes when the leaves prematurely fall off. In Europe only the Cowberry has been noticed as its teleutospore-host, but in the United States it is recorded on eight other species of *Vaccinium* (including *V. Myrtillus* A. Gray); strange to say, the fungus has not yet been observed on the Fir in America. Besides *Abies pectinata*, it is recorded in this country on *A. Nordmanniana* (from Wales, etc.), and the acidia



Fig. 36. *Calyptospora Goeppertiana*. An affected branch of *Vaccinium Vitis-idaea*, Scotland (slightly reduced); a, leaf of *Abies pectinata*, b, leaf of *A. Nordmanniana*, with acidia, Torquay (the latter reduced).

have occurred or been produced artificially elsewhere on at least 10 other species of the genus. A good account is given in the *Kew Bulletin* (1907) from which and other sources the following is drawn.

The most noticeable effect is produced upon the Cowberry. The æcidiospores ripen in July and August, and if one of them is carried to a young branch of the Cowberry, its germ-tube penetrates through a stoma (or, it is said, bores its way through the outer epidermis wall), and penetrates into the cortex, where it grows and next spring extends itself into the new shoots. These present a remarkable appearance: the internodes are lengthened, they become spongy and strongly swollen and coloured red or pink, afterwards turning brown (Fig. 36). The infested plants are taller than uninfested ones and have smaller leaves. The mycelium perennates

in the affected shoots, and passes each spring into the newly formed ones; thus the diseased branches usually occur in clusters. Finally the mycelium penetrates into the epidermis, and the teleutospores are formed within the epidermal cells

which they completely fill. They are mostly divided by two crossed walls into groups of four cells, each provided with a germ-pore at its upper and inner corner.

In the spring following their formation, they germinate *in situ* about May, sending out their basidia through the dead epidermis, and producing their basidiospores in the air. These are blown by the wind on to the just-starting shoots of Fir, and infect the young leaves, on which they produce the æcidia on yellow spots in two rows, one on each side of the midrib. The æcidia are cylindrical, white, with torn margin, $\frac{1}{2}$ —1 mm. high, filled with orange spores, and when empty look like the remains of insects' eggs. Their spores are soon ripe and can infect the young Cowberry shoots, but not the Fir. The diseased leaves soon turn yellow and begin to fall off during July; it is this early defoliation of the Fir that does the harm.

There is obviously no cure except to remove and burn the infested Cowberry plants, and for the sake of prevention these should be searched for in the neighbourhood, when a plantation of Silver Fir or its allies is going to be made. There is no difficulty in detecting them on account of the peculiar appearance which they present. The disease is rare in this country, and is confined mainly to the moorland districts.

These life-histories have been selected in such a way as to show, so far as could be done from British species, the remarkable variations that exist in the cycle of development and in the occurrence of the different spore-forms of the Uredinales.

CHAPTER V

SPECIALISATION

The Uredinales are strictly parasitic (obligate parasites). Many parasitic Fungi can live for a time saprophytically, but those belonging to the present group are quite incapable of such an existence. They are wholly dependent upon their host. Moreover, a study of the evolution of the Uredinales shows us that they have sprung from some simple beginning (resembling perhaps remotely the Ustilaginales) in such a way that new forms ever appeared as new hosts were evolved, and advanced *pari passu* with them. The lowest forms are those parasitic upon the Ferns, the highest are among those on the Compositæ and others of the more specialised orders.

Each form is more or less closely adapted to its particular host, but there is a wide range among them in this respect. A species which can find sustenance upon hosts of more than one kind is called plurivorous. One of the widest is *Puccinia Malvacearum*, confined, indeed, to the Mallow family, but appearing to spread to nearly every genus of the group Malveæ of that family. It has been experimentally shown that it can be transferred from *Malva* to *Althæa* and *vice versâ*, and observations on its occurrence in nature imply that it can pass equally to other genera (see under that species). Or a species may be found only on part of a subfamily, as *P. Arenariæ* on many genera of the Alsineæ. Others are confined to a single genus, but appear to be equally at home on almost any species belonging to it, as *P. Violæ*. Still others are restricted so far as we know to a single species, as *P. Buxi*, and various species

of a genus may have totally distinct rusts upon them, as in the genus *Galium*. So far there is nothing that would contravene one's expectations, but it is impossible to avoid a little incredulity when one is told that on *Hieracium* there is a *Puccinia* which is confined strictly to a single form of a variety of a subspecies of a species of that genus (Probst, 1909).

These specialisations can be proved only by artificial cultures. Certain experimenters have developed very successful methods of infecting given plants with the spores. The acidio- or uredospores are the handiest for this purpose. A sorus of mature uredospores is removed from the leaf, placed in a drop of water and broken up with a needle; the spores are then thoroughly shaken up with a suitable quantity of distilled water. The soil, in which the plant to be used is growing, should have been well watered before the experiment begins. The leaves to be inoculated are first sprayed with distilled water from an atomiser, and then the liquid containing the spores is similarly sprayed upon them, naturally upon a surface which possesses stomata. The plant is then placed under a bell-glass for 24—48 hours or longer, and afterwards kept in a greenhouse at a suitable temperature, protected if required by a larger glass shade with sufficient ventilation. A similar uninoculated plant should be kept near it as a control. In spraying, too great a quantity of moisture should be avoided; in nature it is observed that the germination of spores succeeds best in a layer of dew, not of rain. The keeping under a closed bell-glass is for the purpose of allowing the germ-tubes to enter the stomata; after that nothing more is required but to grow the plant in the ordinary way. The result of the infection will begin to appear in about 10—20 days or more, according to the species.

The inoculation with teleutospores which are ready to germinate may be effected in the same way; or a leaf with mature teleutospores may be tied, spores downwards, on the plant at the selected spot, and left to itself or protected for a time with a layer of wet cotton wool. If it be required to discriminate, under special circumstances, between the artificial infection and any accidental one that might occur, the leaf to be used may be marked with lines in waterproof ink, and the

spores carefully placed between the lines with a camel-hair brush.

A few instances of specialisation will now be given, in addition to the less complicated cases which are treated of under the several species in the systematic part. It will be seen that greater economic importance attaches to this specialisation than might at first be imagined. The first example taken will be that of *Puccinia graminis*, which is found upon various grasses, especially upon cultivated cereals. In the early days of this study almost any rust upon corn was called *P. graminis*; afterwards it was found that there are several kinds, which can be easily separated by their form or colour, and the real *P. graminis* is distinguished as Black Rust, on account of the conspicuous black striæ which its teleuto-sori form upon the culms in autumn. Its uredospores also can easily be distinguished from the uredospores of the other species which live upon the corn. But even after restricting the application of the name by these morphological distinctions, the species is still recorded on more than 180 kinds of grass, although of course some few of these records may be erroneous.

When discussion took place in the past upon the mode by which epidemics of Corn-rust were caused, apart from the Barberry, year after year, it was considered sufficient to point to this wide prevalence of the species, and to assert that it lived through the winter upon the wild grasses and passed from them to the corn when the time arrived. Eriksson is the experimenter who has done most to refute this idea; by making artificial inoculations he has proved that in certain cases the rust which is found on wild grasses will not infect the wheat and *vice versâ*. In spite of this biological difference, however, in most cases no morphological distinctions can be detected, or, if so, they are very slight and somewhat variable. Nevertheless the difference exists, though in varying degrees of definiteness; exactly the same kind of specialisation has been proved to exist in the Erysiphaceæ. The natural explanation is that the species, *P. graminis*, was originally parasitic on numerous grasses, quite indifferently; but as time went on, certain reasons, perhaps geographical or ecological, caused some sets of individuals to

restrict themselves to a particular species of grass; in course of years they became more and more closely adapted to this host, and in so doing grew less and less able to infect other species. But possibly they have seldom completely lost this power, as is shown by the existence of "bridging" species of which Ward produced the best evidence in *P. bromina*; these will be referred to later.

It is assumed that all the forms of *P. graminis* will infect the Barberry; the restrictions are confined to the alternate host. As a result of his experiments, Eriksson divided the species into the following "special forms," which are here called "biological" races:—

1. f. *Secalis*—on Rye
2. f. *Avenae*—on Oat
3. f. *Tritici*—on Wheat
4. f. *Airae*—on *Aira*
5. f. *Agrostidis*—on *Agrostis*
6. f. *Poae*—on *Poa*.

Race 1 grows not only on Rye, but also on *Hordeum vulgare*, *H. murinum*, *Agropyron repens*, *A. caninum*, *Elymus arenarius*, *Bromus secalinus* etc. (In all these enumerations non-British species will be omitted.)

Race 2, on Oat, and on *Arrhenatherum elatius*, *Dactylis glomerata*, *Alopecurus pratensis*, *Milium effusum*, *Bromus arvensis*, *B. madritensis*, *Festuca Myurus*, *F. sciuroides*, *F. ovina* (*tenuifolia*).

Race 3, on Wheat, but also though more rarely on Barley, Oat, and Rye.

Race 4, on *Aira caespitosa*.

Race 5, on *Agrostis canina*, *A. stolonifera*, *A. vulgaris*.

Race 6, on *Poa compressa*, *P. caesia*, *P. pratensis*.

A seventh Race, f. *Hordei*, is sometimes added, though Eriksson included it under his f. *Tritici* or f. *Secalis*.

Jaczewski (1910) from numerous inoculation-experiments arrived at somewhat different results: he found that he could infect Rye only from *Agropyron repens*, *A. caninum*, *Bromus secalinus*, and *Dactylis glomerata*; Wheat only from *A. repens*, *Festuca gigantea*, and *Lolium perenne*; Oat only from

Arrhenatherum elatius, *Alopecurus pratensis*, *Avena p. pilosiuscula*, and *Festuca ovina*, and Barley only from *Triticum* and *Lolium perenne*. According to him it seems that only Barley and Wheat could infect each other directly, although it is known from other sources that Wheat can also infect Rye; this could, however, be done even according to Eriksson's statements, if *Agropyron repens* were employed as a "bridging" species.

Carleton, in North America, experimented with much the same forms, but reached a still different result. According to him (1899) there are only two biological races:

1. f. *Tritici*—on Wheat, Barley, *Hordeum murinum*, *Koeleria cristata*, *Festuca gigantea*, *Dactylis glomerata*, *Agrostis alba*.
2. f. *Avenae*—on Oat, *Avena pratensis*, *A. fatua*, *Hordeum murinum*, *Dactylis glomerata*, *Koeleria cristata*, *Arrhenatherum elatius*, *Holcus mollis*, *Ammophila arenaria*, *Alopecurus pratensis*.

In a further publication (1904) he adds to form (1) that *Holcus lanatus* should probably be included, and furthermore that there is a form of *P. graminis* on *Agrostis alba vulgaris* which could not be transferred to Wheat or Oat.

Freeman and Johnson (1911) in the U. S. cultivated *P. graminis* by its uredospores alone for two years without any loss of vigour. They found that the uredospores of f. *Tritici* would infect Barley easily, rarely Rye, and never Oat, but by using Barley as a "bridging" species, they could infect, with the uredospores produced on that, Rye easily, and Oat in a less degree. The uredospores of f. *Hordei* would infect Wheat and Barley easily, and in a less degree Oat and Rye. The uredospores of f. *Secalis* would infect Barley, and by using that as a "bridging" species would infect Oat at the second step, but in a less degree. The most specialised form was f. *Avenae*; besides the Oat its uredospores would infect only Barley, and not always that.

From this it is evident that either (1) the specialisation of these races is less sharp than Eriksson would have us believe, or (2) the specialisation is taking place along two distinct lines in the United States and in Europe respectively. Probably both of these statements are true, but in support of the former

view we may adduce the fact that Eriksson could infect *Berberis vulgaris* with teleutospores obtained from many grasses (Wheat, Oat, Barley, Rye, *Arrhenatherum elatius*, *Agropyron repens*, *A. caninum*, *Dactylis glomerata*, *Agrostis stolonifera*, *Elymus arenarius*, *Poa compressa*, *P. pratensis*, *Aira caespitosa*, *Bromus secalinus*, and many others, non-British) while Bolley was able to infect a large number of the grasses with spores taken from a single Barberry hedge.

The economic importance of the matter lies in the fact that, if the specialisation is as strict as Eriksson maintains, the corn-crops cannot often (in the absence of *Berberis*) be infected by rust on other cereals or on the wild grasses in the neighbouring hedges. This excessive strictness, however, no one else is prepared to admit: in any case there are obviously plenty of "bridging" species which would enable the rust to get at the corn at the second step, if not at the first. The reason why we cannot, so far, attribute any very great accuracy to the statements regarding specialisation is that the conditions required for infection are demonstrably very complex and at present ill-understood, so that a negative result, even when repeatedly occurring, often proves nothing whatever. This is manifest from Eriksson's own complaints about the "capriciousness" of the germination of the spores, and from the frequent recurrence of such remarks as this—"Uredospores from *Aira caespitosa* would not always infect *Aira caespitosa*." There is another very important conclusion that can be drawn from this survey, viz. that the life-histories of heterœcious rusts must always be worked out separately for each country in the world.

A second example of specialisation is given by the Yellow or Golden Rust (*P. glumarum*): it is divided by Eriksson into five biological races:

1. f. *Tritici*—on Wheat alone
2. f. *Hordei*—on Barley alone
3. f. *Secalis*—on Rye (perhaps also on Wheat)
4. f. *Elymi*—on *Elymus arenarius* alone
5. f. *Agropyri*—on *Agropyron repens*,

but of the last Eriksson remarks that he could not infect this host with its own uredospores. With the exception mentioned,

Arrhenatherum elatius, *Alopecurus pratensis*, *Avena pubescens*, and *Festuca ovina*; and Barley only from *Triticum* and *Lolium perenne*. According to him it seems that only Barley and Wheat could infect each other directly, although it is known from other sources that Wheat can also infect Rye; this could, however, be done even according to Jaczewski's statements, if *Agropyron repens* were employed as a "bridging" species.

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2. f. *Avenae*—on Oat, *Avena pratensis*, *A. fatua*, *Hordeum murinum*, *Dactylis glomerata*, *Koeleria cristata*, *Arrhenatherum elatius*, *Holcus mollis*, *Ammophila arenaria*, *Alopecurus pratensis*.

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5. f. *Glyceriae*—on *G. aquatica*
6. f. *Agropyri*—on *A. repens*
7. f. *Epigaei*—on *Calamagrostis epigeios* (also, but rarely, on *Avena sativa*)
8. f. *Holci*—on *Holcus lanatus*.

To these Mühlenthaler (1910) adds a ninth form, on several species of *Bromus*. These results agree pretty well with those of Klebahn, but not with those of Carleton. According to the latter, the only host of *P. Lolii* in nature, in the United States, is *Avena sativa*: but in artificial cultures it can be foisted on other species because of the unnatural conditions, especially on account of the employment of very young and non-resistant plants. In any case, however, there is a general agreement that the form of *P. Lolii* on *Avena sativa* cannot be transferred to Wheat, Barley, or Rye. In fact, with the exceptions mentioned, it was found by all experimenters more or less in all these cases, that attempts made to transfer the fungus from the host of one "special form" to those of the others were unsuccessful from some unknown cause.

The state of things in regard to the two common *Uromyces* species, found upon Grasses, is more perplexing. There is no agreement whatsoever between the various authors who have experimented upon them. The latest results are, perhaps, the following:

Krieg (1909) divides *Uromyces Dactylidis* into two biological races or "formæ speciales":

1. f. sp. with æcidium on *Ranunculus bulbosus*, *R. repens*
2. f. sp. with æcidium on several non-British species of *Ranunculus*.

Juel (*Svensk Bot. Tidskr.* ii. 169, 1908) divides *Uromyces Poae* into nine biological races, of which the following seven may be British:

1. f. sp. *Ficariae-nemoralis*
2. f. sp. *Ficariae-trivialis*
3. f. sp. *Ficariae-pratensis*
4. f. sp. *repentis-nemoralis* (also on *R. bulbosus*)
5. f. sp. *repentis-trivialis* (also on *Poa annua*)
6. f. sp. *repentis-pratensis*
7. f. sp. *auricomæ-pratensis*.

The hosts of these are indicated by their names, but there is a very high probability that their distinction depends entirely on accidents of weather or manipulation at the time when the inoculation was made.

Finally, in regard to another case, *P. dispersa* (sens. lat.) the Brown Rust of Corn, it will be seen by referring to the systematic part that it is divided into a number of subordinate forms or sub-species, which are for the most part only distinguishable biologically: though here the amount of difference is much greater than in *P. graminis*, and there is more to be said in favour of calling these forms distinct species, as is often done. For, as will be seen by the descriptions, in some of them an æcidium stage is known, in others not, though Klebahn remarks that in the latter cases we might possibly find the æcidium, if we could trace each form to its ancestral home. Moreover, in some of these cases, the teleutospores germinate in the spring, in others in the autumn.

One of the most remarkable of these forms is *P. bromina*, on species of *Bromus*, from which Ward (1902) obtained such important results. For instance, he showed that uredospores taken from *B. mollis* always infected *B. mollis* and *B. secalinus* and their close allies, but not *B. sterilis* and its allies; while on the other hand those on *B. sterilis* would infect *B. sterilis* and its ally *B. madritensis*, but rarely the other Bromes. We can reason, as Ward says, that uredospores from *B. mollis* infect that species readily "because their food-supplies and previous environment have affected their protoplasm in some way which makes it easier for their germ-tubes and mycelium to grow in tissues which afford them the same nutriment and present the same obstacles, as they have hitherto enjoyed or been confronted with" (p. 299). They can flourish in *B. secalinus* because here also the food-supplies etc. offered are nearly the same. But in *B. sterilis* the resistance of the plant to infection is sufficiently great to present a barrier which is incapable of being overcome except by an odd spore, here and there, varying from the normal. In 4, out of 148, trials, uredospores from *B. mollis* infected *B. sterilis* and these might then produce spores which could pass on to *B. madritensis*, although in no single

case out of many experiments could *B. madritensis* be infected directly from *B. mollis*. *B. sterilis* therefore acted as a "bridging" species, and enabled the parasite to pass from *B. mollis* to *B. madritensis*, though it could not do so without this intervention. The same existence of "bridging" species has been demonstrated in *Erysiphe graminis*, and no doubt will be found in numerous other instances.

Ward further mentions (1903) that he found *B. arduennensis* var. *villosus* to be infectible by the spores from *B. sterilis*, *B. mollis*, and *B. patulus*, as well as by those from *B. arduennensis*, and therefore easily able to serve as a bridging species between these others. Nevertheless, that such intermediary species do not exist in all cases is proved by the fact that when he grew "more than 200 species and varieties of *Bromus* side by side or intermingled in contiguous beds, certain species invariably caught the disease and became rusted, while others close by showed no sign of infection."

The occurrence of these abnormal spores, i.e. mutations, which is proved in the case of *Bromus*, is of great significance and gives us the clue by which we can understand how a gradual or sudden passage can take place, and has taken place, from one host to another, so that now an appreciable percentage of the modern vegetable world have parasites more or less specialised to themselves.

Another important consequence follows from this fact of specialisation. If the parasite is so narrowly adapted to its particular host, it may be expected that varieties of the host can be found or bred which will be able to resist attack, that is, will be *immune*. A great deal of research has been devoted of late years, especially by Professor Biffen of the Agricultural School at Cambridge, to this subject of breeding a race of wheat which will be immune to Rust, and a certain amount of progress has been made. Immunity depends chiefly (perhaps entirely) upon the ability of the cytoplasm of the host-cells to resist infection by secreting anti-toxins which will kill the mycelium of the fungus. Immunity and susceptibility (which, however, seem to be always relative only and not absolute) have been proved to be inherited, and in fact to be Mendelian

characters, the latter being dominant (Biffen, 1907, 1912; Pole-Evans, 1911). But owing to the minute specialisation which is characteristic of many Rusts, a variety may be immune to one Rust while susceptible to another, or may even be immune in one country but susceptible to the same Rust in a different climate. The latter change would depend upon a slight disturbance (by climatic factors) of the delicate balance which existed between the attacking and resisting powers of the two organisms.

It may be pointed out here that this affords an opportunity for dealing a final blow at the moribund "mycoplasma" hypothesis. For when a susceptible and an immune variety of wheat were crossed (Biffen, 1905) *both the reciprocal crosses* were susceptible. Yet in that cross in which the pollen used was taken from the susceptible parent, while the other was immune, the only means by which the "mycoplasma" could be conveyed would be in the generative nuclei of the pollen-tube, which is inconceivable. An attempted criticism of this conclusion (Butler, 1905) misses altogether the point of the argument: the maternal parent could not be classed as immune, if it usually contained the "mycoplasma" already in its tissues.

CHAPTER VI

CLASSIFICATION AND PHYLOGENY

The Uredinales form a group of Fungi so closely allied that they must be regarded as monophyletic. The number of species considered in the present work is about 250. They may be divided into five families.

A. IMPEDICELLATÆ.

I. Melampsoraceæ—Teleutospores not pedicellate, but seated on a dilated hyphal cell, produced singly in the tissues of the host, or compacted side by side into flat crusts, 1—4-celled. Germination by an external basidium, with minute round basidiospores (about 10μ). Uredospores abstricted singly. *Æcidia* with or without a peridium.

II. Cronartiaceæ—Teleutospores not pedicellate, produced in chains, which are either separate or united into columnar, wart-like, or lens-shaped bodies. Germination as in I. Basidiospores round, small (about 10μ or less).

III. Coleosporiaceæ—Teleutospores in one (or rarely two) layers, forming waxy, bright-coloured crusts, not pedicellate, but seated on a dilated hyphal cell, at first one-celled. Germination by the formation of an internal basidium of four superimposed cells, each of which protrudes a sterigma and a large basidiospore (about 20μ).

IV. Endophyllaceæ—*Æcidio*-teleutospores surrounded by a hemispherical peridium and produced from a fusion-cell, in chains with intercalary cells, but germinating with an external basidium.

B. PEDICELLATÆ.

V. Pucciniaceæ — Teleutospores distinctly pedicellate though the pedicel is often very short or caducous, united into pulvinate sori, easily separable or immersed in gelatine, each spore consisting of one or more cells arranged in rows or groups. Germination by an external basidium: basidiospores more or less ovate. *Æcidia* with or without peridium. Uredospores always abstricted singly on distinct pedicels.

The following genera belonging to these families are British, excluding *Uredinopsis*:

MELAMPSORACEÆ.

A. Teleutospores composed of 2—4 laterally adherent cells, the septa in the latter case cruciately arranged.

a. Teleutospores colourless, scattered singly in the host-tissues or formed in the epidermal cells. On Ferns.

- [1. Teleutospores extracellular, scattered. Uredospores surrounded by a peridium, colourless, without germ-pores. *Uredinopsis*.]
2. Teleutospores intracellular. Uredospores surrounded by a peridium, colourless, without evident germ-pores. *Milesina*.
3. Teleutospores intracellular. Uredospores without (or with a very rudimentary) peridium, yellow, with germ-pores.

Hyalospora.

b. Teleutospores brownish, in the epidermal cells or forming subepidermal crusts. On Seed-plants.

1. Teleutospores intracellular. *Æcidiospores* without smooth spot. *Calyptospora*.
2. Teleutospores intracellular. *Æcidiospores* smooth on one side. *Thecospora*.
3. Teleutospores extracellular, subepidermal. *Æcidiospores* smooth on one side. *Pucciniustrum*.

B. Teleutospores one-celled, united into crusts.

a. Teleutospores in the epidermal cells, usually one-celled, faintly coloured. Uredospores with peridium, but without paraphyses, and without evident germ-pores. *Æcidium* with a peridium. *Melampsorella*.

b. Teleutospores not intracellular, one-celled, brown.

1. Teleutospores subepidermal. Uredo- and *æcidiospores* as above. *Melampsoridium*.
2. Teleutospores subepidermal or subcuticular. Uredospores without peridium, but with paraphyses. *Æcidium* of the *cicoma* type. *Melampsora*.

CRONARTIACEÆ.

- A. Teleutospores in pulvinate sori. *Chrysomyxa.*
 B. Teleutospores in columnar sori. *Cronartium.*

COLEOSPORIACEÆ.

- A. Basidiospores fusiform. Uredospores formed singly. *Ochropsora.*
 B. Basidiospores ellipsoid or lemon-shaped. Uredospores in chains. *Coleosporium.*
Æcidia with an inflated peridium.
 C. Basidiospores globose. Basidium ultimately protruded. Teleutospores with lateral pedicel. *Zaghouania.*

ENDOPHYLLACEÆ.

- Æcidio-teleutospores in a cup-shaped peridium, germinating with an external basidium. *Endophyllum.*

PUCCINIACEÆ.

- A. Teleutospores embedded in gelatine, on Gymnosperms. No uredospores. *Gymnosporangium.*
 B. Teleutospores free, on Angiosperms.
 a. Teleutospores of more than two cells.
 1. Teleutospores of many cells. No uredospores. *Xenodochus.*
 2. Teleutospores of several cells, dark-coloured. Cæomata encircled by paraphyses; uredospores the same and with paraphyses intermixed. *Phragmidium.*
 3. Teleutospores of several cells, faint-coloured. Cæomata without paraphyses; uredospores often with them. *Kuehneola.*
 4. Teleutospores of three radiating cells. *Triphragmium.*
 b. Teleutospores of one or two cells.
 1. Teleutospores of two cells, usually. *Puccinia.*
 2. Teleutospores of one cell. *Uromyces.*

PHYLOGENY.

In trying to comprehend the phylogenetic evolution of this group of Fungi, there are several landmarks which can be borne in mind. In the first place, their strict parasitism implies a very close adaptation between them and their hosts: this is not only *a priori* probable, but is confirmed by culture-experiments and the existence of biological races. Therefore those which are parasitic on the lowest hosts must be, on the whole, most similar to the primitive forms, and those parasitic

on the higher families would be expected to show the greatest advance. This consideration alone is sufficient to determine that *Uredinopsis* is like one of the primitive Uredinales and that the genera *Puccinia* and *Uromyces* contain the highest types. For *Uredinopsis* grows upon Ferns, and more than a quarter of the *Pucciniæ* live on the Compositæ.

Secondly a comparison of the spores of these two genera and their respective allies suggests that the possession of a single definite and well-formed germ pore is a characteristic of the latest forms, while the primitive ones had no germ-pores at all, but protruded the germ-tube, as a conidium usually does, at any convenient point or where the wall first gives way. There is reason, from another point of view, to conclude that germ-pores, when first existing, were numerous and indefinitely scattered. A gradual reduction in their number and their restriction to definite parts of the spore-wall occurred during the course of evolution. The æcidio-teleutospore of *Endophyllum* has no germ-pore; in the Pucciniacæ the æcidio-spores have usually several indistinct ones, the uredospores have them fewer and more easily visible, and the teleutospores have one or a small number, oftentimes very plainly marked.

Amongst the other Fungi, the group which presents the nearest approach to the Uredinales is that of the Ustilaginales, which are also parasites; their teleutospores (brandspores), in the family Ustilaginacæ, germinate in a similar way, but with less definiteness, by the formation of a basidium and basidiospores. It may be inferred that this particular feature is one of the most deeply seated characters of both groups, and is therefore inherited from their ancestors.

Moreover, this feature is exhibited in the Uredinales by cells which belong to the sporophytic generation, and after a certain amount of growth the mycelium produced by the basidiospores bears the two kinds of gametes. An exactly similar course of events takes place in certain Algæ, e.g. *Griffithsia*, where the sporophyte bears tetraspores which on germination produce a thallus which bears gametes. It is true that in the Red Algæ the tetraspores are more usually arranged in tetrahedral fashion, but other modes also obtain, among them

(in *Corallina*) an arrangement of four superposed cells as in the "basidium" of the Uredinales. Moreover in one of the groups of the latter, the *Coleosporiaceæ*, as well as in *Gleropsora*, this division into four cells takes place within the spore-mother-cell not outside it. It is a reasonable tentative hypothesis that this "internal" formation of the four cells is the primitive mode inherited from the predecessors of the groups and that the formation of an "external" basidium is a later adaptation of their successors to their environment. This would lead one to look for the ancestors of the Uredinales among the Red Algae.

The obvious implication is that the *Coleosporiaceæ* retain much of the Uredinal primitive character and this is corroborated by the fact that the æcidial host of *Coleosporium* is in every case, so far as known, a species of *Pinus*. The telentospore-host may belong to the *Compositæ* or various other families, it is true, but it is now generally admitted that the æcidial host is the primitive, and that the others have been adopted by successive mutations. It has an important bearing on this argument that, in *Gallowaya Pini*, the telentospores which are of exactly the same nature as in *Coleosporium* are borne on a Pine (*Pinus inops* Ait.).

Again, it has been shown that it is possible, without violence, to interpret the female-cells of the æcidium as furnished with a trichogyne, such as the carpogonia of the *Floridææ* possess, though in the Uredinales (possibly as a consequence of their terrestrial habit) it has become abortive. Trichogynes are not uncommon in other groups of Fungi—in certain Ascomycetes, in the *Laboulbeniaceæ*, and among the Lichens, in *Collema* and other genera. Moreover in *Collema* the trichogyne and correlative spermatia are almost certainly functional (Bachmann, 1912); the same is true in the *Laboulbeniaceæ*, but in most Ascomycetes the trichogyne has either been lost altogether, or if it survives has lost its function.

In order that the trichogynes in the ancestral Uredinales should be effective, the female gametes must have been situated beneath a stoma. It is a suggestive fact that in certain of the group, belonging to the lowest forms, the sori of various kinds

are always, or usually, so placed. For instance, in *Melampsorium betulinum* the teleuto-sori almost invariably originate directly below the stomatal pore. The cause of this cannot be merely the need of oxygen for respiration, since it has been shown that the intercellular spaces of a leaf are all well supplied in that respect. Fig. 37 is drawn from the lower epidermis of a leaf of *Betula alba* in which teleuto-sori were just beginning to be produced. The same thing is true of the teleuto-sori of *Melampsora Larici-epitea* and other *Melampsorae*, and apparently even of *Phragmidium*. In others of the lower groups, *Uredinopsis*, *Milesina*, etc., uredo-sori are equally so placed, both



Fig. 37. *Melampsorium betulinum*. a, young sori of teleutospores, viewed through the epidermis, showing how they originate beneath a stoma; at the lower right-hand is a sorus with only two teleutospores, $\times 300$; b, three young teleutospores, forming a similar sorus, seated on a common base, $\times 600$.

primary uredo-sori (which represent æcidia) and secondary. It can be justifiably inferred that this was the primitive position in which the female gametes and afterwards the other kinds of spore-sori were formed at the beginning: in *Puccinia* and its allies this position is no longer maintained.

Since in the Ustilaginales (a comparatively non-progressive, if not degraded, group) there is only one kind of spore besides the basidiospore and the ensuing conidia, and this is produced irregularly and not in definite sori, it may be inferred that the same was true of the primitive Uredinales. This one kind of spore must have been the equivalent of the teleutospore. It is

found that, in *Uredinopsis*, the teleutospores are irregularly scattered throughout the spongy mesophyll of the host. But, in this position, their germination, or at least the liberation of their basidiospores, could not take place easily until the leaf had decayed. The transference to a place either (1) beneath the cuticle, (2) in the epidermal cells, or (3) just beneath the epidermis, and their aggregation into definite sori which by their upward pressure would burst through the overlying layers, would both be an advance in adaptation; so these various positions are found to be occupied in successive genera, and the most effective of all (the subepidermal sorus) is alone to be met with in the highest groups.

In regard to a peridium, this can be supposed non-existent at first, (1) because there is no peridium in the Ustilaginales, (2) because a peridium could not exist so long as the trichogyne was functional.

Here, it is true, there is a little deviation from what might be expected; a peridium is found in *Uredinopsis*, *Milesina*, *Melampsorella* and *Melampsoridium* (round the uredo-sori), but in *Hyalospora* this is very rudimentary or completely absent, and it can scarcely be compared, in any case, with the peridium of the æcidial stage of *Puccinia*, being of a very different character. It must be considered as a special development, separately originated for the protection of the uredo-sori in these lower groups. When one considers the acidiospores, one finds them in the intermediate types either without a peridium, or with encircling paraphyses, or with an irregularly shaped peridium, and it is only in the higher forms, such as *Puccinia* and *Uromyces*, that the beautifully outlined "Cluster-cup" arises.

In respect to these higher groups it has been shown elsewhere (Grove, 1913) that the Endophyllaceae constitute the starting-point from which the varied forms of the Pucciniaceae have been evolved. A certain amount of advance went on, of course, simultaneously among the Impedicellatae, though to nothing like the same extent.

In *Endophyllum* the acidiospore which is the product of the fusion-cell is also the teleutospore which germinates with a basidium: in accordance with theory it is accompanied by

spermogones. The first stage of evolution was the separation of this spore-form into two, one (the acidiospore) germinating conidially, the other (the teleutospore) following it and germinating basidially: types approximating to this stage are seen in the section Pucciniopsis. It is quite certain that uredospores are only modified acidiospores, formed as a mere multiplying device without the intervention of another fusion-cell. The peridium which is found in these later stages of evolution round the æcidium was at first represented (doubtless even in the primitive *Endophyllum*) by a mere circle of paraphyses or not at all.

From a cytological point of view, the fusion of the two nuclei in the teleutospore may be taken as paralleled by the similar fusion in the basidium of the Basidiomycetes; the division into four basidiospores follows in both cases, although the mechanism is different. If the view propounded in a previous chapter is adopted, that the four cells of the "basidium" of the Uredinales are the real tetraspores¹ and the basidiospores are merely conidia whose function is to facilitate dispersion by wind, it will be seen that the difference in the Basidiomycetes consists in the fact that cell-walls are not formed round the tetraspores previously to the production of conidia. This may recall the fact that in the Red Algæ the four spores in a tetrasporangium are also not surrounded by cell-walls before their discharge into the water. Of course, in the subaërial Uredinales and Basidiomycetes such naked masses of protoplasm would be comparatively ineffective for propagation, and are here replaced by methods more suitable to a land environment. The throwing off of the basidiospores with a jerk appears to be the same in both these groups.

A similar comparison with the Ascomycetes cannot be made with equal advantage, until the students of that group of Fungi have come to some semblance of agreement as to the actual course of its cytological history. But it is impossible to overlook the remarkable parallelism between the cytology of the

¹ In the Himalayan *Barclayella*, which is placed among the Melampsoraceæ (?), these tetraspores are said to round themselves off and separate, apparently as the normal mode, without forming basidiospores.

Uredinales, as now known, and that attributed by Claussen (1912) to *Pyronema confluens*. In his paper, which is a conclusive reiteration and confirmation of his earlier work, he shows that the numerous male nuclei of the antheridium enter the ascogonium, and in it pair with the numerous female nuclei, but *without fusing with them*. These synkarya then pass out into the ascogenous hyphæ, and there multiply by numerous conjugate divisions. Finally a pair of descendants of these nuclei are seen in the young ascogenic-cell, one being male and the other female: here they divide conjugately into two pairs, one pair being the *ascus-nuclei*, and the other pair *reserve-nuclei* which may repeat the process in several ways. The two non-sister ascus-nuclei fuse; then the fusion-nucleus divides, the first division being heterotypic (meiotic, reducing, possessing synapsis and diakinesis stages) and the two following ones, by which eight spores are formed, being homotypic. There is thus in the life-cycle a single fusion, followed by a single reduction. The ascus is a spore-mother-cell, comparable to the teleutospore of the Uredinales, but forming an *octad*, not a *tetrad* of spores. The two "reserve-nuclei," left after the formation of the ascus, answer to the two nuclei left in the "basal" cell of the æcidium. Compare in this respect especially the process as it takes place in *Endophyllum*. The sporophyte generation consists then in *Pyronema* only of the ascogenous hyphæ, whose cells contain the diploid number of chromosomes though arranged within two nuclear membranes.

In certain species of *Laboulbenia* (Faull, 1912) there is a similar cytological history. The ascogenic hyphæ contain two nuclei which divide homotypically by conjugate division, and two non-sister nuclei pass into each ascus where they fuse; the two left in the ascogenic cell may repeat the process. The fusion-nucleus of the ascus divides to form eight nuclei of which four soon degenerate: the first division is meiotic and the others homotypic. There is no double fusion in this group and the same statement may justifiably be inferred to be true of other Ascomycetes.

On the other hand, Harper (1900), Blackman, Welsford, Fraser, Brooks, Carruthers (1911) and others, maintain that in

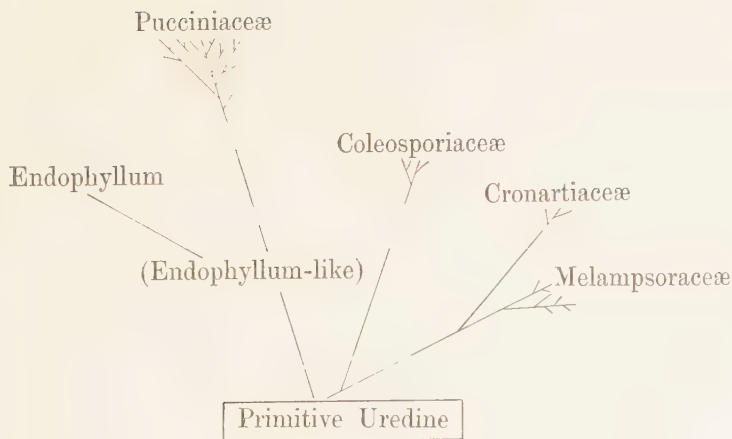
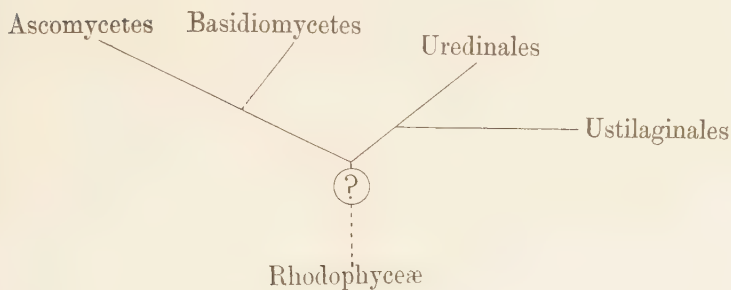
Pyronema confluens and in many other members of the Ascomycetes there is a double fusion (one in the ascogonium and one in the young ascus), followed by a double reduction in the ascus during the formation of the eight spores, the first division being *meiotic*, the second *homotypic*, and the third *brachymeiotic*. In view of the established relationship between the Ascomycetes on the one hand and the Uredinales and Basidiomycetes on the other, this idea seems to be very unlikely. If correct, the double process is a special development, peculiar to some only of the Ascomycetes. The matter can only be decided by fresh investigations, but it seems in all probability that the hypothesis of a second fusion and subsequent brachymeiosis is the result merely of a misinterpretation of the observed phenomena.

According to Lutman (1910), in the Ustilaginales most of the cells of the mycelium are binucleate, but the perfect resting spores are always uninucleate, as are the cells of the basidia.

Rawitscher (1912) says the same, and adds that the conjugate condition arises (according to the species) by the anastomosis in pairs either of the basidium-cells, or of the basidiospores, or of the cells of the mycelium produced by them, and the passage of the nucleus of the one cell into the other to form a sinkaryon.

Finally, it may be pointed out that the ideas embodied in the foregoing discussion are in harmony with the now generally accepted doctrine of the polyphyletic origin of the Fungi, by which it is assumed that their various groups are not derived from one or two ancestors, but originated separately from distinct sub-divisions of the Algae, much in the same way in which (on a smaller scale) the non-chlorophyllose Phanerogams have arisen from various orders or families of Flowering Plants. From this point of view, according to which the vast majority of the Fungi originated from the Red Algae, it is not without significance that already some of that group are known which (though still rightly classed as Algae) have assumed a true holoparasitic habit—a statement which cannot be made to the same extent, if at all, about other algal groups. Examples are found in the well-known *Harveyella mirabilis* (Sturch, 1899) and in *Choreocolax Polysiphoniae* (Richards, 1891).

From these considerations the probable phylogeny of the Uredinales may be represented as in the following schemes.



NOTE ON MANIPULATION.

Dried specimens of Uredinales keep most of their characters unchanged for an unlimited time, but the colours fade except those of the teleutospores. The only two difficulties found in examining them are in regard to the markings on the outer surface of the spores, and the number of germ-pores. For the first, different methods succeed in different cases, but the finer markings can usually be seen by examining the spores under a one-sixth inch in air, or in water after squeezing out their granular contents by tapping or pressing hard upon the cover-glass. For the second, boiling for about a minute in a drop of lactic acid, on a glass slide over a spirit-lamp, is the best course, although expulsion of the contents under pressure frequently brings the germ-pores into view; in fact so plain do they often become that they can be photo-micrographed with ease. Boiling in lactic acid also restores old collapsed spores to their former size and plumpness.

The preparation from which Fig. 37 was drawn was obtained in the following way: lay the side of the leaf opposite to the sori in a thin layer of 5 % KOH solution for an hour or so, then reverse and brush or scrape away the softened tissue as far as possible; on mounting the remaining surface, epidermis upwards, in glycerine and water, the arrangement of the parts can be clearly seen.

If it is wished to observe the germination of the spores in a hanging drop, almost any uredo will serve; for teleutospores *Puccinia Malvacearum* and for æcidiospores *Æcidium Ficariae* are usually the most handy. One of the best double stains to use is Diamant Fuchsin and Light Green; the former stains the nuclei red and the latter the cell-walls green. Stain heavily with the former and wash out with alcohol till the desired tint is arrived at; then use the Light Green dissolved in clove oil.

UREDINALES

A group of Fungi which are obligate parasites on ferns and the higher plants. Mycelium filamentous, branched, septate, developed within the tissues of the host, producing teleutospores (resting spores, chlamydospores) which on germination give rise to a generally four-celled "basidium," each cell of which may in turn produce, on a sterigma, a single basidiospore (conidium). In addition, there are often produced spermatia (in spermogones), æcidiospores (in æcidia), and uredospores (in sori).

PUCCINIACEÆ

PUCCINIÆ. Teleutospores of one or two cells, scarcely gelatinous (except the pedicels in some foreign species). { *Uromyces*.
Puccinia.

PHRAGMIDIÆ. Teleutospores of more than two cells, the walls of the pedicels subgelatinous.

Teleutospores more or less verrucose.

{ *Triphragmium*.
Phragmidium.

Teleutospores nearly or quite smooth.

{ *Kuehneola*.
Xenodochus.

GYMNOSPORANGIÆ. Walls of pedicels of teleutospores becoming highly gelatinous.

{ *Gymnosporangium*.

UROMYCES Link.

Autœcious or heterœcious.

Spermogones deeply embedded in the tissues of the host, flask-shaped with conical mouth and ostiolar filaments. Æcidia with an evident, usually cup-shaped peridium; æcidiospores with indistinct germ-pores. Uredospores formed singly on their pedicels, with several usually rather distinct germ-pores which are often surrounded by a thickened border, rarely accompanied by paraphyses. Teleutospores one-celled, on distinct pedicels, almost always with an apical germ-pore. Basidiospores flattened on one side or kidney-shaped.

The species are arranged according to the families to which the hosts belong; see *Puccinia*. This genus is often considered the most highly (at least the latest) evolved of the Uredinales; but rather it forms a heterogeneous group, the species of which have arisen at different times from various species of *Puccinia*.

1. *Uromyces Valerianæ* Fekl.

Uredo Valerianæ Schum. Pl. Säll. ii. 233.

Æcidium Valerianearum Duby, Bot. Gall. ii. 908. Cooke, Handb. p. 540; Micr. Fung. p. 196.

Lecythæa Valerianæ Berk.; Cooke, Handb. p. 532; Micr. Fung. p. 222.

Uromyces Valerianæ Fekl. Symb. Myc. p. 63. Plowr. Ured. p. 128.

Sacc. Syll. vii. 536. Sydow, Monogr. ii. 19. Fischer, Ured. Schweiz, p. 54, f. 41.

Spermogones. Epiphyllous, in small clusters, honey-coloured, turning black.

Æcidiospores. *Æcidia* hypophyllous, and often on the nerves, petioles and stalks, seated on pale thickened spots, densely aggregated or circinate, cup-shaped, whitish-yellow; margin revolute and torn; spores covered with minute crowded warts, yellow, $18-25 \times 16-20 \mu$.

Uredospores. Sori amphigenous, usually on indefinite yellow spots, scattered or aggregated here and there, minute, punctiform, pulverulent, brown; spores globose to broadly ellipsoid, verrucose-echinulate, yellowish-brown or brown, $21-28 \mu$; epispore $2\frac{1}{2}-3 \mu$ thick, with two or three germ-pores.

Teleutospores. Sori similar, but longer covered by the epidermis, dark-brown; spores ellipsoid or ovate, with a flat subhyaline papilla at the summit, smooth, pale clear-brown $20-30 \times 13-21 \mu$; epispore thin, scarcely thickened above; pedicels short, thin, hyaline, rather deciduous.



Fig. 38. *U. Valerianæ*. Teleutospores and uredospore (the latter viewed dry) on *V. officinalis*.

On *Valeriana dioica*, *V. officinalis*. *Æcidia* in May and June; uredospores from June, teleutospores from July to October. Common. (Fig. 38.)

The uredospores seem to be variable in their markings; some are distinctly verrucose with pointed warts; others are as distinctly echinulate.

DISTRIBUTION: Europe and South Africa.

2. *Uromyces Scrophulariæ* Fekl.

Æcidium Scrophulariæ DC.; Cooke, Handb. p. 544; Micr. Fung. p. 199.

Uromyces Scrophulariæ Fekl. Symb. Myc. p. 63. Plowr. Ured. p. 139. Sacc. Syll. vii. 559. Sydow, Monogr. ii. 27. Fischer, Ured. Schweiz, p. 75, f. 56.

U. concomitans B. et Br.; Cooke, Micr. Fung. p. 213.

Spermogones. Few, singly or in little groups, simultaneously with the æcidia.

Æcidiospores. Æcidia hypophyllous or on the stems, on yellowish spots, in rounded clusters or in more or less elongated patches on the nerves and stems, cup-shaped, yellowish; margin involute, entire; spores verruculose, smooth below, yellowish, $18-21 \times 14-18 \mu$.

Teleutospores. Sori small and roundish, arranged like the æcidia except that they form more elongated groups (as much as 10 cm. long) on the stems, long covered by the lead-coloured epidermis, at length naked and pulverulent, dark-brown; spores very irregular, obovate, fusiform, or ellipsoid, angular, rarely sub-globose, apex rounded, truncate or slightly pointed, somewhat thickened (up to 6μ), with a dark-coloured cap, attenuated below, smooth, brown, $18-35 \times 11-18 \mu$; pedicels persistent, hyaline or yellowish, nearly as long as the spore.

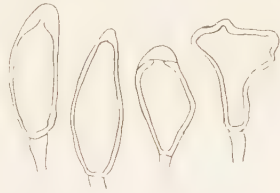


Fig. 39. *U. Scrophulariæ*. Teleutospores on *S. aquatica*.

On leaves, petioles and stems of *Scrophularia aquatica*, *S. nodosa*. July—September. Not common. (Fig. 39.)

The spots on the leaves are pallid, edged with violet-brown. The teleutospores especially cause considerable distortion of the leaves and stems. The two kinds of spores may be produced on the same mycelium, and the æcidia and teleuto-sori can occur simultaneously and intermixed, or the latter surrounding the former (Grevillea, iii. 181, pl. 36). For this

is one of the species in which it is stated (Dietel, Flora, 1895, lxxxi. 396), that the æcidiospores can reproduce the æcidia. Spermogones are found sparingly only with the first generation of the æcidia and at the same time. The secondary æcidiospores, in fact, take the place of uredospores.

DISTRIBUTION : Europe generally.

3. *Uromyces Limonii* Lév.

Æcidium Statices Desm. ; Cooke, Micr. Fung. p. 197 ; Grevillea, i. 7.
Uromyces Limonii Lév. Dict. Hist. Art. Ured. p. 19. Cooke, Handb. p. 518 ; Micr. Fung. p. 212. Plowr. Ured. p. 122, p.p. Sacc. Syll. vii. 532 p.p. Sydow, Monogr. ii. 41.

Æcidiospores. *Æcidia* amphigenous, often on red or brownish spots, in roundish clusters or elongated along the nerves, usually shortly cylindrical, whitish, with a torn margin ; spores densely and minutely verruculose, yellowish, $21-32 \times 18-26 \mu$.

Uredospores. Sori amphigenous, scattered, generally roundish or, on the stem, oblong, long covered by the epidermis, at length naked, pulverulent, cinnamon ; spores varying from globose to oblong, densely verruculose with minute papillæ, yellowish-brown, $22-32 \times 20-28 \mu$; epispore $1\frac{1}{2}-2\frac{1}{2} \mu$ thick, with two or three germ-pores.

Teleutospores. Sori amphigenous or caulicolous, scattered or circinate, roundish or oblong, long covered by the epidermis, pulvinate, black ; spores subglobose or more frequently oblong or clavate, sometimes rounded, sometimes attenuated at the apex, where the wall is up to 10μ thick, attenuated below, smooth, brown, $24-50 \times 14-25 \mu$; pedicels as much as 80μ long, thick, pale-brownish, persistent.

Fig. 40. *U. Limonii*. Teleutospores and uredospore.

On leaves and stems of *Statice Limonium*. Not common. *Æcidia* in June and July ; uredo- and teleutospores from July to October. (Fig. 40.)

This species was formerly united with *U. Armeriæ* (q.v.), but the teleutospores are distinctly different.

DISTRIBUTION: Europe, North Africa, Siberia and North America.

4. *Uromyces Armeriæ* Lév.

Caeoma Armeriæ Schlechtd. Fl. Berol. ii. 126.

Uromyces Armeriæ Lév. Ann. Sci. Nat. sér. 3, viii. 375. Sydow, Monogr. ii. 40. Fischer, Ured. Schweiz, p. 52, f. 39.

U. Limonii Plowr. Ured. p. 122 p.p. Sacc. Syll. vii. 532 p.p.

Spermogones. Scattered among the æcidia, honey-coloured.

Æcidiospores. Æcidia amphigenous, scattered or in small clusters, at first hemispherical, then cup-shaped, with a whitish incised margin; spores densely and minutely verruculose, yellow, $17-28 \times 16-22 \mu$.

Uredospores. Sori amphigenous, sometimes on purplish spots, rounded or elongated, surrounded or half-covered by the cleft epidermis, pulverulent, cinnamon; spores globose to oval, very densely and minutely verruculose, yellowish-brown, $24-32 \times 21-28 \mu$; epispore $2\frac{1}{2}-3 \mu$ thick, with two or three germ-pores.

Teleutospores. Sori similar, dark-brown; spores globose to ovate, rounded and thickened (7μ) at the apex, with a broad flat cap, usually rounded below, smooth, brown, $24-36 \times 21-32 \mu$; pedicels hyaline, nearly as long as the spore, seldom persistent.

On leaves and peduncles of *Armeria maritima*. Not uncommon. Æcidia in May and June; uredospores from June onwards; a few teleutospores begin to appear in the uredo-sori towards the end of July. (Fig. 41.)



Fig. 41. *U. Armeriæ*.
Teleutospore and uredospore.

This species was united by Plowright with *U. Limonii*, but is distinguished by the more readily pulverulent sori, the shorter and broader teleutospores, and the shorter hyaline pedicel which is easily detached. The distinctness of the two species does not seem, however, to have been tested by experimental cultures. Though the uredo- and teleutospores

have occurred for many years consecutively on Thrift in my garden, I have never noticed the æcidia; the uredospores last through the winter on the evergreen leaves, and reproduce the fungus about June; teleutospores are rather scarce.

DISTRIBUTION: Central and North-Western Europe.

5. *Uromyces Trifolii* Lév.

Puccinia Trifolii Hedw. f. in DC. Flor. fr. ii. 225.

Uromyces Trifolii Lév. Ann. Sci. Nat. ser. 3, viii. 371. Plowr. Ured. p. 124 p.p. Sacc. Syll. vii. 534 p.p. Sydow, Monogr. ii. 132.

Fischer, Ured. Schweiz, p. 23 p.p.

Trichobasis fallens Cooke, Micr. Fung. p. 226 p.p.

Puccinia fallens Cooke, Handb. p. 508 p.p.

Nigredo fallens Arthur, N. Amer. Fl. vii. 254.

Uredospores. Sori hypophyllous and on the petioles, and like those of *U. Trifolii-repentis*; spores differing in having 5—7 germ-pores.

Teleutospores. Indistinguishable from those of *U. Trifolii-repentis*.

Fig. 42. *U. Trifolii*.
Uredospores on *T.*
pratense.

On *Trifolium hybridum*, *T. incarnatum*, *T. medium*, *T. pratense*. Not com-

mon. (Fig. 42.)

Liro proved by culture-experiments that the *Uromyces* on *Trifolium repens* could not be transferred to *T. hybridum* or *T. pratense*. Since this difference is accompanied by the absence of the æcidium in the latter species and by a difference in the number of the germ-pores, they are considered distinct by Sydow. But on *Trifolium pratense* I have found uredospores with not more than four germ-pores, each covered with a low flat hyaline cap. In that case only the absence of the æcidium would separate the two forms, though the average number of germ-pores is no doubt different in the two cases.

An æcidium has been found elsewhere on *T. pratense*, but this has been experimentally proved (Dietel, Flora, 1895, lxxxi. 398) to belong to another European and North American species, *U. minor* Schröt. = *U. oblongus* Vize (Grevillea, v. 110), which has no uredospores, but only æcidio- and teleutospores.

Cooke's species, *U. apiculatus* (Grevillea, vii. 136), is indefinite; the form on clover may belong here, that on *Lathyrus pratensis* to *U. Pisi*.

DISTRIBUTION: Europe, Asia Minor, Persia, North America, etc.

6. **Uromyces Trifolii-repentis** Liro.

U. Trifolii-repentis Liro, Act. Soc. Faun. Flor. Fenn. xxix. 15. Sydow, Monogr. ii. 131. Fischer, Ured. Schweiz, p. 23, f. 19.

U. Trifolii Plowr. Ured. p. 124 p.p. Sacc. Syll. vii. 534 p.p. McAlpine, Rusts of Australia, p. 97, f. 142, & pl. G, f. 32.

Trichobasis fullens Cooke, Micr. Fung. p. 226 p.p.

Puccinia fullens Cooke, Handb. p. 508 p.p.

Nigredo Trifolii Arthur, N. Amer. Fl. vii. 255.

Spermogones. Epiphyllous, honey-coloured, forming minute clusters.

Æcidiospores. *Æcidia* hypophyllous, in clusters, roundish on the leaves and as much as 5 mm. long on the nerves and petioles, shortly cylindrical, whitish-yellow; margin white, torn, hardly revolute; spores minutely verruculose, yellowish, $17-21 \times 14-18 \mu$.

Uredospores. Sori hypophyllous and on the petioles, scattered over the leaves or gregarious, small or rarely confluent and larger, soon naked, pulverulent, pale-brown; spores globose, ovate or ellipsoid, echinulate, yellow-brown, $19-26 \times 17-24 \mu$; epispore about $1\frac{1}{2} \mu$ thick, with two to four (generally two) equatorial germ-pores.

Teleutospores. Sori surrounded by the cleft epidermis, similar, but elongated on the petioles, and darker brown; spores globose to ovate, rounded at the apex, with a very small hyaline papilla, smooth or at times bearing a few minute warts arranged more or less in lines, brown, $18-30 \times 16-25 \mu$; epispore about 2μ thick; pedicels short, thin, hyaline, deciduous.



Fig. 43. *U. Trifolii-repentis*. a, æcidia on young leaf; b, uredo- and teleuto-sori, on later-formed leaf.

On leaves and petioles of *Trifolium repens*. *Æcidia* (rare) from April and uredospores from May onwards. (Fig. 43.)

This species is distinguished from *U. Trifolii* Lév. by the smaller number of germ-pores of the uredo, and also by the presence of the æcidia, which cause long crooked swellings on the petioles and nerves, but not on

the leaves. The mycelium of the æcidial stage is said to be perennial in the host; Dietel says that in some localities the æcidiospores can reproduce themselves, and that then the uredo is suppressed.

Both this species and the preceding are distinguished from *U. flectens* in the fact that the sori are smaller, distributed more uniformly over the leaf, and do not cause distortions.

The æcidium is rare in Britain (I have seen specimens only from Perth); most of our records of *Uromyces* on *T. repens* belong to the following common species, *U. flectens*. *Pseudopeziza Trifolii* (a Discomycete) is common on leaves of white clover and is not infrequently mistaken for the uredo-stage of *U. Trifolii-repentis*, but is distinguishable by its being confined to the upper surface of the leaves. No practical means of prevention are known for either the Clover Rust (*Uromyces*) or the Clover Leaf-spot (*Pseudopeziza*).

DISTRIBUTION: Europe, Asia Minor, Persia, North and South America, Australia.

7. *Uromyces flectens* Lagerh.

Uromyces flectens Lagerh. Svensk Bot. Tidskrift, iii. 36. Sydow, Monogr. ii. 360. Grove, Journ. Bot. 1911, p. 366.
Puccinia neurophila De Toni, Sacc. Syll. vii. 698.

Teleutospores. Sori hypophyllous, or more often on the nerves and petioles where they cause swellings and distortion, scattered, rather large, $\frac{1}{2}$ —2 mm. long or even confluent and larger, long covered by the epidermis, then pulverulent, dark-brown; spores as in *U. Trifolii-repentis*.

Fig. 44. *U. flectens*.
Teleutospores on *T. repens*.

On *Trifolium repens*. May—October.
Common. (Fig. 44.)

It has been frequently noticed that the *Uromyces* on *Trifolium repens* behaves differently in different localities; sometimes forming teleutospores only, from May to October; at others forming both æcidia and uredospores during the same time. Plowright records an interesting experiment which he performed (Ured. p. 125); in October he brought a plant of *T. repens*, with the *Uromyces* upon it, indoors and kept it there till the following summer. During all this time it produced only teleutospores. Lagerheim, in 1909, noticing that the form which produced only teleutospores had sori which were larger, more predominant upon nerves and petioles, and remained longer covered by the epidermis, described this as a distinct

species, to which evidently Plowright's specimen may be ascribed. Cooke's figure of his *U. apiculosa*, on *Trifolium repens* (Micr. Fung. pl. vii. f. 154), is probably the same species.

DISTRIBUTION: Middle Europe and Persia.

8. *Uromyces striatus* Schröt.

Uredo apiculata var. *Trifolii* Strauss, Ann. Wett. ii. 97 p.p.

Uromyces striatus Schröt. Abhandl. Schles. Ges. 1872, p. 11. Sacc. Syll. vii. 542 p.p. Sydow, Monogr. ii. 115. Fischer, Ured. Schweiz, p. 31, f. 24. Cf. Plowr. Ured. p. 134.

[*Spermogones* }
Æcidiospores } . As in *Uromyces Pisi*.]

Uredospores. Sori amphigenous, scarcely ever on the nerves, without spots, scattered, occasionally aggregated and confluent, minute, pulverulent, cinnamon; spores globose to ellipsoid, faintly and sparsely echinulate, yellowish-brown, $15-22\ \mu$; epispore $1\frac{1}{2}-2\ \mu$ thick, with 4—6 or even more germ-pores, each with a small hyaline cap.



Fig. 45. *U. striatus*. a, two teleutospores on *T. minus* (ex herb. Broome); b, a teleutospore on *T. arvense* (foreign, ex herb. De Thümen); c, uredospore from the same leaf as a.

Teleutospores. Sori similar, but darker; spores globose to ovate, with a minute and narrow papilla, striated from apex to base by longer or shorter lines of warts, brown, $18-24 \times 15-20\ \mu$; epispore $1\frac{1}{2}-2\ \mu$ thick; pedicels short, hyaline, deciduous.

[*Æcidia* on *Euphorbia Cyparissias*, not known in Britain;] uredo- and teleutospores on leaves and stems of *Trifolium minus*. Bath (Herb. Broome); King's Norton (Worcestershire). Very uncommon. July—August. (Fig. 45.)

See remarks made about the æcidial stage under *U. Pisi*. Schröter proved the connection of an æcidium on *Euphorbia Cyparissias* with an exactly similar *Uromyces* on *Trifolium agrarium*. *U. striatus* is found elsewhere on *Trifolium procumbens* and also on many species of *Medicago*,

including all the British species, but I have seen no specimens on these from this country. The teleutospores on *T. minus* which I have observed are more distinctly verrucose and less striated than in the figures given by Fischer, and may possibly not belong to the same species.

DISTRIBUTION: Europe, North and South America, East Indies.

9. *Uromyces Loti* Blytt.

Uromyces Loti Blytt, Christ. Vidensk.-Selskabs Forhandl. 1896, p. 37.

Sydow, Monogr. ii. 110. Grove, Journ. Bot. 1911, p. 367.

U. Euphorbiae-Corniculati Jordi, Centralbl. f. Bakt. 1904, 2. xi. 791.

Fischer, Ured. Schweiz, p. 34, f. 26.

[*Spermogones*. Hypophyllous, numerous, scattered amongst the æcidia.

Æcidiospores. Æcidia distributed uniformly over the lower surface of the leaf, cup-shaped, with a torn white revolute



Fig. 46. *U. Loti*. Four teleutospores, all on *L. corniculatus*; a shows how the spores look when wet, the others are viewed dry.

margin; spores densely and minutely verruculose, orange, 18—23 μ .]

Uredospores. Sori amphigenous, but mostly hypophyllous, scattered, minute, round, sometimes confluent, surrounded by the cleft epidermis, soon naked, pulverulent, cinnamon; spores globose to ellipsoid, with short blunt and rather distant spines, brownish, 17—25 $\times$ 16—23 μ ; epispore $2\frac{1}{2}$ —3 μ thick, with 2—5 germ-pores.

Teleutospores. Sori similar, but darker in colour; spores globose to obovate, often with a low flat pore-cap at the apex, which is not thickened, beset with minute warts and ridges which are often arranged in undulating longitudinal lines, brown, 17—25 $\times$ 14—21 μ ; pedicels short, hyaline, deciduous.

[*Æcidia* on *Euphorbia Cyparissias*;] uredo- and teleutospores on *Lotus angustissimus*, *L. corniculatus*; July, August. (Fig. 46.)

Plowright refers to this species (but not as British) in a note on p. 134. The markings on the teleutospore are very delicate and can scarcely be seen except when the material is fresh and the spores are viewed dry. I found that the longitudinal lines of warts were more strongly marked and anastomosed more frequently on spores from *L. corniculatus* than from *L. angustissimus* (Newquay, Cornwall), on which they were fainter and more irregular, but this difference may have been partly due to the fact that the latter had been gathered (by Dr Vigurs) many years before they were examined. Jordi proved that *æcidiospores* from *E. Cyparissias* would freely infect *L. corniculatus*. But see *U. Pisi*.

DISTRIBUTION: Western, Central and Southern Europe, and Japan.

10. *Uromyces Anthyllidis* Schröt.

Uredo Anthyllidis Grev. in Sm. Eng. Fl. v. 383.

Uromyces Anthyllidis Schröt. Hedwig. xiv. 162. Plowr. Ured. p. 135. Sacc. Syll. vii. 551. Sydow, Monogr. ii. 64. Fischer, Ured. Schweiz, p. 36, 543, f. 28.

Uredospores. Sori amphigenous, widely and irregularly scattered, or sometimes with a circle of small ones round a larger one, minute, roundish, black and shining, soon naked, then pulverulent, cinnamon; spores globose or subglobose, sparsely and finely echinulate, yellowish-brown, $18-25\mu$; epispore $3-3\frac{1}{2}\mu$ thick, with 4—6 germ-pores (4—5, Bubak; 5—8, Fischer).



Fig. 47. *U. Anthyllidis*. Uredospore.

Teleutospores. Sori similar, but darker in colour. Spores globose to ovate, with a minute papilla at the rounded apex, verrucose, brown, $16-22 \times 15-20\mu$; epispore rather thick; pedicels short, hyaline, deciduous.

On leaves of *Anthyllis Vulneraria*. Not common. June—October. (Fig. 47.)

It is probable that this species occurs only on *A. Vulneraria* (and on the continent, *A. maritima*), but it has many close allies on other Leguminosæ. Teleutospores are rarely formed; in specimens gathered in mid-September I have found only one or two, in the midst of abundant

uredospores. The warts on the teleutospores are not numerous and are rather easy to see.

DISTRIBUTION: North-western and Middle Europe.

11. *Uromyces Ervi* Westendorp.

Æcidium Ervi Wallr. Fl. Crypt. Germ. ii. 247.

Uromyces Ervi Westd. Bull. Acad. Roy. Sci. Belg. xxi. pt. 2, p. 246, f. 3.

Plowr. Ured. p. 140. Sydow, Monogr. ii. 96. Fischer, Ured.

Schweiz, p. 69, f. 53.

Æcidiospores. *Æcidia* amphigenous, or on the petioles, solitary or 2—8 together in little scattered groups, cup-shaped, whitish; margin faintly revolute, scarcely torn; spores densely and minutely verruculose, pale-yellowish, $16-25 \times 14-18 \mu$.

Uredospores. Sori rarely formed, amphigenous or on the petioles and stems, scattered, minute, oblong, surrounded by the ruptured epidermis, cinnamon; spores ovate or ellipsoid, distantly echinulate, brownish-yellow, $20-30 \times 18-22 \mu$, with two (rarely three) germ-pores.

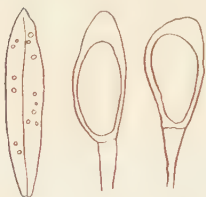


Fig. 48. *U. Ervi*. Leaf of *E. hirsutum*, with *æcidia*, slightly enlarged; two teleutospores.

Teleutospores. Sori amphigenous, or more frequently on the petioles and stems, scattered, minute, oblong, surrounded by the ruptured epidermis, blackish-brown; spores subglobose to obovate, usually darker and rounded above (where the wall is up to 8μ or more thick), rounded or attenuated at the base, smooth, brown, $20-28 \times 14-20 \mu$; pedicels brownish, persistent, as long or twice as long as the spore.

On leaves, petioles, and stems of *Ereum hirsutum* (*Vicia hirsuta*). *Æcidia*, May—October; teleutospores from July onwards, lasting through the winter on the dead stems. (Fig. 48.)

It has been proved by many culture experiments that Plowright was correct in his belief that this species is strictly confined to the one host. The *æcidiospores* are capable of reproducing the *æcidium* and are found throughout the season; the *uredospores* are, perhaps in consequence, not abundant, only a few being occasionally found and usually intermixed with teleutospores.

DISTRIBUTION: Europe, Japan.

12. **Uromyces Fabæ** De Bary.

Uredo Fabae Pers. in Röm. Neu. Magazin, i. 93.

Uromyces Fabae De Bary, Ann. Sci. Nat. ser. 4, xx. 72. Plowr. Ured. p. 119. Sacc. Syll. vii. 531 p.p. Sydow, Monogr. ii. 103. Fischer, Ured. Schweiz, p. 65, f. 49—51. McAlpine, Rusts of Australia, p. 93, f. 307.

Trichobasis Fabae Cooke, Handb. p. 508; Micr. Fung. p. 225.

Uromyces appendiculatus Lév.; Cooke, Micr. Fung. p. 212, pl. vii. f. 149—150 p.p.

Puccinia Fabae Link, referred by Cooke to this species, has no existence in nature (Handb. p. 508; Micr. Fung. p. 211).

Spermogones. Hypophyllous, growing among the æcidia.

Æcidiospores. Æcidia hypophyllous, seated on pale-yellow spots, solitary or in small round or elongated clusters, shortly cup-shaped, with a whitish, torn, revolute margin; spores densely and minutely verruculose, yellow, 14—22 μ .

Uredospores. Sori amphigenous, scattered or circinate, girt by the ruptured epidermis, minute, pulverulent, pale-brown; spores globose to ovate, distantly echinulate, at length pale-brown, 20—30 $\times$ 18—26 μ ; epispore 1½—2½ μ thick, with three or four germ-pores.

Teleutospores. Sori similar, but persistent and darker or blackish-brown; spores subglobose to obovate, rounded or truncate and thickened above, where the wall is dark and 7—11 μ thick, sometimes with a colourless papilla, smooth, brown, 25—38 $\times$ 18—27 μ ; pedicels brownish, persistent, thick and as much as 40—70 μ long.

On leaves and stems of *Faba vulgaris*, *Lathyrus pratensis*(?), *Pisum sativum*, *Vicia Cracca*, *V. sativa*, *V. sepium*. Æcidia in April, May; uredospores from May, teleutospores from July onwards, lasting through the winter on the dead stems. (Figs. 49—52.)



Fig. 49. *U. Fabae*.
Teleutospores on stem
of Broad Bean.

One of the most widely spread of the Uredinales, occurring in every

part of the world; reported on many Leguminosæ, but doubtless some of these are distinct species. Jordi has distinguished under *U. Fabae* three



Fig. 50. *U. Fabae*. Teliospores and uredospore on *Vicia Cracca*.

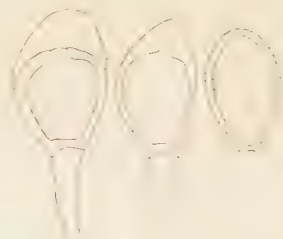


Fig. 51. *U. Fabae*. Teliospores and uredospore on *Vicia sepium*.

“biological” races—(1) on *Faba vulgaris* and *Pisum sativum*, (2) on *Lathyrus vernus* and probably also on *Pisum sativum*, (3) on *Vicia Cracca*, *Pisum sativum*, and possibly also *Vicia hirsuta*.

The æcidial generation is frequent on some hosts, such as *Vicia sepium* and species of *Lathyrus*. On *Faba vulgaris* and *Pisum sativum* it is, on the contrary, very rare, being recorded by Sydow, on the Pea, only from Norway, East Indies and Japan (once from each). It has been seen on the Bean in the East Indies, but seems to be not uncommon in artificial cultures, in which Plowright produced it both on Pea and Bean from the same teliospores (Plowr. Ured. p. 121).

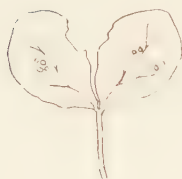


Fig. 52. *U. Fabae*. Æcidia on Pea, from Plowright's culture, in which he produced them on both Pea and Bean from the same teliospores.

On the leaves of the common field Bean only the uredospores are generally to be found, even as late as mid-October, but on the stems the teliospores form large black sori. On *Vicia sepium* the uredo-sori are often darker and covered by the epidermis for a shorter time than on the Bean, while the telio-sori occur in great abundance on the leaves and even on the tendrils.

If all the infected haulm, etc., were burnt instead of being put on the manure heap or left to rot on the ground, the disease would become less prevalent, especially if Jordi's idea is true, that the Rust on the wild Vetches is a distinct biological race. In Ecuador, at Quito, which has a very equable climate of “perpetual spring,” *U. Fabae* has, according to Lagerheim, become almost an isolated uredo. The same thing is true of it in other tropical climes.

DISTRIBUTION : world-wide.

13. **Uromyces Orobi** Lév.

Æcidium Orobi Pers. in Röm. Neu. Magazin, i. 92. Cooke, Handb. p. 542; Micr. Fung. p. 197.

Uromyces Orobi Lév. Ann. Sci. Nat. ser. 3, viii. 371, 376. Plowr. Ured. p. 121. Sydow, Monogr. ii. 106. Fischer, Ured. Schweiz, p. 69, f. 52.

Spermogones. Hypophyllous, mixed with the æcidia.

Æcidiospores. Æcidia hypophyllous, on yellowish spots, in dense clusters 1—5 mm. long, rarely solitary, shortly cup-shaped, with whitish revolute margin; spores densely and minutely verruculose, yellowish, 14—21 μ .

Uredospores. Sori amphigenous, scattered, minute, punctiform, pulverulent, brown; spores globose to ovate, distantly echinulate, pale-brown then darker, 20—28 $\times$ 18—25 μ ; epispore 3—4 μ thick, with three or four germ-pores.

Teleutospores. Sori similar, but darker; spores subglobose to ovate, rounded or sub-conical above, and much thickened (7—11 μ) and darker, smooth, brown, 25—35 $\times$ 18—28 μ ; pedicels persistent, yellowish, thick, as much as 100 μ long.

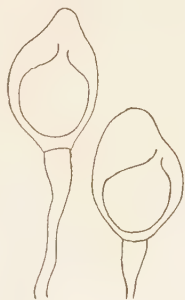


Fig. 53. *U. Orobi*.
Teleutospores on
O. tuberosus.

On *Orobis tuberosus* (*Lathyrus montanus* = *L. macrorrhizus*). Æcidia in May and June; uredo- and teleutospores from June onwards. (Fig. 53.)

Cooke says that the æcidia also occur on the stems. The thicker membrane of the uredospores, which is also less strongly echinulate, distinguishes them from those of *U. Fabae*. Jordi made attempts to infect various other species of *Lathyrus*, and also species of *Vicia* and *Pisum*, from *U. Orobi*, but in every case without success.

DISTRIBUTION: North-western and Central Europe.

14. **Uromyces Pisi** Wint.

Uredo appendiculata var. *Pisi* Pers. Obs. Myc. i. 17.

Æcidium Cyparissiae DC. Flor. fr. ii. 240.

Uromyces Lathyri Fekl. Symb. Myc. p. 62.

U. Pisi Winter, Krypt. Flor. i. 163. Cooke, Grevillea, vii. 135. Plowr.

Ured. p. 133. Sacc. Syll. vii. 542 p.p. Sydow, Monogr. ii. 124.

Fischer, Ured. Schweiz, p. 28, f. 22.

Spermogones. Hypophyllous, numerous, scattered amongst the æcidia.

Æcidiospores. Æcidia distributed uniformly over the lower surface of the leaf, cup-shaped, with a white, torn, broadly revolute margin; spores densely and minutely verruculose, orange, $18-23\ \mu$.

Uredospores. Sori generally hypophyllous, scattered, minute, soon naked, pulverulent, cinnamon; spores globose or subglobose, minutely verruculose, yellow-brown, $21-25\ \mu$ diam.; epispore $1\frac{1}{2}-2\frac{1}{2}\ \mu$ thick, with 3-5 germ-pores.



Fig. 54. *U. Pisi*.
a, æcidia and s,
spermogones on
leaf of *Euphorbia*
Cyparissias
(from the Dover
specimen).

Teleutospores. Sori similar, but sometimes confluent and larger, dark-brown; spores subglobose to ovate, with a small hyaline papilla (as much as $3\ \mu$ high), everywhere minutely and rather densely verruculose, brown, $20-28 \times 14-22\ \mu$; epispore $1\frac{1}{2}\ \mu$ thick; pedicels hyaline, short, deciduous.

Æcidia on *Euphorbia Cyparissias*, May, June; uredo- and teleutospores on *Pisum sativum* and *Lathyrus pratensis*, July—September. Rare. (Fig. 54.)

Although both will equally infect *E. Cyparissias*, it is probable that the *Uromyces* on *Pisum* is biologically distinct from that on *Lathyrus*. It is not certain that the latter has been found in this country, but the former is recorded from various places. It must be remembered that *U. Fabae* occurs also on the same two genera, though all the spore-forms of the two can be easily distinguished.

An æcidium on *E. Cyparissias*, and attributed to *U. Pisi*, was found at Dover, May, 1909 (Rev. T. Taylor); the specimen is in the British Museum, but there is no proof that this belonged to *U. Pisi*, because it has been shown that *U. Loti*, *U. striatus* (both of which are British), as well as two other (non-British) species, equally produce on *E. Cyparissias* æcidia which are morphologically indistinguishable. This æcidium possesses a perennial mycelium, which permeates the whole host and deforms and bleaches it. The connection of one form of it with *Uromyces Pisi* has been experimentally demonstrated by Schröter, Rostrup, Fischer and others. The *Uromyces* on *Vicia Cracca* which was formerly considered to

belong to *U. Pisi* has been proved by Jordi to be confined to that species and not to be transmissible to *Pisum sativum* or *Lathyrus*. It has been named by Magnus *U. Fischeri-Eduardi*, but is not known as British.

DISTRIBUTION: Europe generally; North America less commonly.

15. *Uromyces Phaseolorum* De Bary.

Æcidium Phaseolorum Wall. Fl. Crypt. Germ. ii. 256.

Uredo appendiculata var. *Phaseoli* Pers. Syn. p. 222.

Uromyces Phaseolorum De Bary, Ann. Sci. Nat. ser. 4, xx. 80 (1863).
Cooke, Grevillea, vii. 135.

U. Phaseoli Wint. Pilze, p. 157 (1884). Plowr. Ured. p. 122. Yorkshire Fung. Fl. p. 186.

U. appendiculatus Link, Obs. ii. 28. Sacc. Syll. vii. 535. Sydow, Monogr. ii. 120. Fischer, Ured. Schweiz, p. 19, f. 16. McAlpine, Rusts of Australia, p. 92, f. 306 (all pro parte).

Nigredo appendiculata Arthur, N. Amer. Fl. vii. 257 p.p.

[*Spermogones*. In little clusters, whitish, then yellowish.

Æcidiospores. *Æcidia* hypophyllous, clustered in little roundish groups 2—3 mm. wide on yellowish or brownish spots, cup-shaped, whitish, with a torn revolute margin; spores polygonal or oblong, densely and minutely verruculose, colourless, $18-36 \times 16-24 \mu$.]

Uredospores. Sori generally hypophyllous, on indistinct spots, scattered or in little clusters here and there, minute, soon naked, surrounded by the cleft epidermis, cinnamon; spores subglobose to ovate, distantly but sharply echinulate, brownish-yellow, $18-28 \times 18-22 \mu$; epispore brownish-yellow, about $1\frac{1}{2} \mu$ thick, with two germ-pores; contents colourless.

Teleutospores. Sori similar, but confluent, larger, amphigenous and blackish-brown; spores subglobose to ovate, rounded above, with a wide germ-pore and a hemispherical hyaline papilla, smooth or rarely provided, especially near the apex, with a few hyaline warts, chestnut-brown, $24-35 \times 18-25 \mu$; epispore up to $3\frac{1}{2} \mu$ thick; pedicels hyaline, rather thin, about as long as the spore.

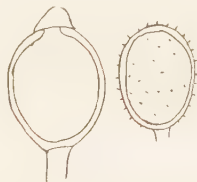


Fig. 55. *U. Phaseolorum*.
Teleutospore and uredospore.

On leaves of *Phaseolus vulgaris*. May, July—October; even earlier on forced plants. Uncommon. (Fig. 55.)

De Bary (*l.c.*) proved the genetic connection of the æcidia with the uredo- and teleutospores. The æcidia are rarely met with; they may occur either before or in company with the other spore-forms. I have seen no proof that they have been found in this country. The description is founded upon that of Sydow. Fischer says that this species is very common in Switzerland on *Phaseolus*; it may become a dangerous parasite on forced Beans. All affected plants (leaves and stems) should be burnt. *U. appendiculatus* of Sydow, which occurs on many Leguminosæ, is probably a collective species, though no experiments bearing on this point are available.

DISTRIBUTION: as a collective species (*U. appendiculatus*) world-wide.

16. *Uromyces tuberculatus* Fekl.

Æcidium Euphorbiae Gmel. in Linn. Syst. Nat. ii. 1473 p.p. Purton, Midl. Flor. iii. 293. Cooke, Handb. p. 537; Mier. Fung. p. 195 p.p. Plowr. Ured. p. 270.

Uromyces excavatus DC.; Cooke, Grevillea, ii. 161; Mier. Fung. p. 213.

U. tuberculatus Fekl. Symb. Myc. p. 64. Sydow, Monogr. ii. 165.

Fischer, Ured. Schweiz, p. 43, f. 33.

U. proeminens Lév.; Sacc. Syll. vii. 553 p.p.

Spermogones }
Æcidiospores } . Hypophyllous, spread uniformly over the whole leaf; æcidia immersed, cup-shaped, with a short denticulate margin; spores orange, densely verruculose, $17-25 \times 14-20 \mu$.

Uredospores. Sori hypophyllous, scattered, at length naked, cinnamon; spores more or less globose, yellowish-brown, aculeolate, $20-25 \mu$; epispore $1\frac{1}{2}-2\frac{1}{2} \mu$ thick, with 5—7 swollen germ-pores (4—5, Fischer).

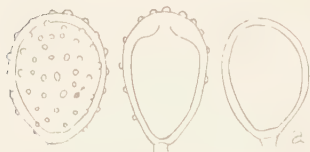


Fig. 56. *U. tuberculatus*. Two mature teleutospores; a, a teleutospore before the tubercles are developed.

Teleutospores. Sori amphigenous and on the stems, round, scattered or sometimes arranged in little groups, pulverulent, blackish-brown or black; spores globose to ellipsoid, occasionally

with a flat, broad, hyaline papilla, at first smooth, then covered with more or less distant, broadly conical, obtuse, subhyaline warts, chestnut-brown, $20-30 \times 18-24 \mu$; epispore $2-2\frac{1}{2} \mu$ thick; pedicels hyaline, deciduous.

On *Euphorbia exigua*. Rare: Hampshire, Mr Hill (Plowr. l.c.): King's Cliffe, Norths. (Grevillea, l.c.). Midlands (Purton, l.c.). (Fig. 56.)

For a long time this species was considered to have only uredo- and teleutospores, but the connection of these with the æcidium occurring on the same species of *Euphorbia* was established by Tranzschel. Berkeley, at King's Cliffe, found them all together. The description given above is partly founded upon those of Tranzschel, Sydow, and Fischer. The mycelium of the æcidial stage infests the whole plant, that of the teleutospores is more or less localised.

DISTRIBUTION: France, Germany, Switzerland.

17. *Uromyces Geranii* Otth et Wart.

Æcidium Geranii DC.; Cooke, Handb. p. 543; Micr. Fung. p. 199 p.p.

Trichobasis Geranii Cooke, Handb. p. 530.

Uromyces Geranii Otth et Wartm. Schweiz. Krypt. no. 401. Cooke,

Micr. Fung. p. 213. Plowr. Ured. p. 126. Sacc. Syll. vii. 535.

Sydow, Monogr. ii. 190. Fischer, Ured. Schweiz, p. 16, f. 14.

Spermogones. Mixed with the æcidia, orange.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, on the leaves chiefly in the vicinity of the nerves and there forming large dense clusters on thickened spots, on the petioles forming elongated clusters and often causing great distortion, at first hemispherical and closed, then opening by a round pore, at length with a very slightly revolute incised margin, orange; spores somewhat ovate, densely and minutely verruculose, yellow, $22-28 \times 18-24 \mu$; epispore rather thick.

Uredospores. Sori hypophyllous, generally on brownish or reddish-yellow spots, scattered or gregarious, minute, rounded, pulverulent, cinnamon, surrounded by the cleft epidermis; spores globose to obovate, sparsely echinulate, brown, $20-30 \times 18-24 \mu$; epispore about 2μ thick, with one (rarely two) germ-pores.

Teleutospores.

Fig. 57. *U. Geranii*.
Teleutospores on *G.*
silvaticum.

Sori similar, but less pulverulent, and blackish-brown; spores subglobose to ovate, not thickened above, but with a hyaline papilla as much as 6μ high, smooth, brown, $22-35 \times 18-25\mu$; pedicels short, hyaline, deciduous.

On *Geranium dissectum*, *G. molle*, *G. pratense*, *G. pyrenaicum*, *G. silvaticum*.
Not common. *Æcidia*, March to June;

teleutospores, June—October. (Fig. 57.)

Liro proved that the æcidium of this parasite from *G. silvaticum* produced uredo- and teleutospores on the same plant, and Bock showed that the uredospores from the same species reproduced themselves on other hosts of the same genus. But there is another æcidium occurring on *G. pratense* and *G. silvaticum*, which belongs to a quite different life-cycle. This is *Æcidium sanguinolentum* Lindr., and is the æcidial stage of the heteroecious *Puccinia Polygoni-amphibii* Pers. (q.v.). It differs from the æcidium of *U. Geranii* in being seated on conspicuous blood-red or deep-purplish spots which are not distinctly thickened; moreover the shape of the spores is that usual in æcidiospores, viz. rounded-polygonal, while those of *U. Geranii* are always more or less ovate, and have a thicker wall.

Again, there is an æcidium on *G. pusillum* which, according to Sydow, is probably also found on *G. molle* and *G. rotundifolium*, and which belongs to *Puccinia Polygoni-Convulvuli* (q.v.)—a form of *P. Polygoni-amphibii* which is often separated as a distinct species. The uredo- and teleutospores would, of course, not follow the æcidium on the same plant in either of these two cases.

On *G. pyrenaicum* there is another *Uromyces* (*U. Kabatianus*) which differs in the arrangement of its sori; see below.

DISTRIBUTION: Europe, except in the extreme South.

18. *Uromyces Kabatianus* Bubák.

Uromyces Kabatianus Bubák, Sitz. kön. böhm. Gesell. Wissen. 1902, p. 1, f. 1—5. Sacc. Syll. xvii. 249. Sydow, Monogr. ii. 194. Fischer, Ured. Schweiz, p. 18, f. 15.

Spermogones. Amphigenous, few, large, honey-coloured, then darker, on the same spots as the æcidia.

Æcidiospores. *Æcidia* hypophyllous, on round yellowish spots, in little clusters 2—4 mm. wide, hemispherical, opening

by a pore: spores roundish-polygonal to oblong-ovate, densely verruculose, yellow, $24-33 \times 18-26 \mu$.

Uredospores. Sori hypophyllous, on yellow spots, in circinate groups, seldom scattered, rather large, pulverulent, chocolate-brown; spores roundish, brown, distantly echinulate, $22-26 \mu$; episore about 2μ thick.

Teleutospores. Sori hypophyllous, on yellowish or reddish



Fig. 58. *U. Kabatianus*. Teleutospores and uredospore, on *G. pyrenaicum*.

spots, rather large, covered with the thin silvery-shining epidermis, generally in circinate groups, soon confluent, pulverulent, brown; spores ovate, often oblong, scarcely thickened above, but with the germ-pore provided with a prominent subhyaline papilla (up to 7μ high), smooth, pale-brown, $22-42 \times 13-20 \mu$; pedicels short, hyaline, deciduous.

On *Geranium pyrenaicum*, and possibly on *G. molle* and *G. pusillum*. (Fig. 58.)

This has been separated by Bubák from *U. Geranii* on the ground of the circinate arrangement of the uredo- and teleuto-sori, and the more oblong and longer teleutospores: the description of the æcidia and teleutospores is taken from that of Bubák. According to Sydow, Lind has succeeded in transferring this species from *G. pyrenaicum* to *G. molle* and *G. pusillum*. Bubák thought that only this form occurred on *G. pyrenaicum*, but Bock (Centralbl. f. Bakt. 2, xx. 584) showed that typical *Uromyces Geranii* could also be produced on that host.

The two *Uromyces* are very closely allied, but several distinctions are alleged: the uredospores themselves are identical, but not the sori; according to Sydow, the teleutospores of *U. Kabatianus* do not appear till towards the end of October, are paler, longer and more oblong in shape with a higher papilla, while their sori are generally circinate, paler and less compact. The teleutospores of *U. Geranii* appear at the beginning of summer, the sori are nearly black, rather compact, and more scattered. I have specimens collected at Cambridge in August, on *G. pyrenaicum*, having the uredo-sori in circinate groups on conspicuous yellow spots, and

containing no teleutospores; it appears probable that these belong to *U. Kabatianus*, which will no doubt be found in many places, if looked for.

DISTRIBUTION: a few places in Europe and Asia Minor.

19. *Uromyces Alchemillæ* Lév.

Uredo Alchemillae Pers. Obs. Myc. i. 98.

Uromyces Alchemillae Lév. Ann. Sci. Nat. 3, viii. 371 (1847). Plowr.

Ured. p. 137. Sacc. Syll. vii. 553. Sydow, Monogr. ii. 196.

Fischer, Ured. Schweiz, p. 44, f. 34.

U. intrusa Cooke, Handb. p. 519; Micr. Fung. p. 213.

Trachyspora Alchemillae Fekl. Bot. Zeit. xix. 250. Arthur, N. Amer.

Fl. vii. 178.

Uredospores. Sori hypophyllous, radially arranged, occupying nearly the whole leaf-surface, rounded or elongated, often confluent and covered by large fragments of the torn epidermis, then pulverulent, orange, yellowish or even whitish; spores ellipsoid to oblong, faintly echinulate, orange or yellowish, $16-25 \times 14-21 \mu$.



Fig. 59. *U. Alchemillae*. Teleutospores on *A. vulgaris*.

Teleutospores. Sori hypophyllous, scattered, rarely confluent, minute, round, pulverulent, brown; spores globose to obovoid or oblong, not thickened above, coarsely warted, brown, $26-40 \times 20-30 \mu$; epispore $2-2\frac{1}{2} \mu$ thick; pedicels hyaline, very deciduous, short or rather long; teleutospores are also formed in the uredo-sori.

On *Alchemilla vulgaris*. Common. Uredospores, April—June; teleutospores, July—October. (Fig. 59.)

The mycelium perennates in the rhizome and grows up with the young leaves, causing them to stand more erect, making them paler and conspicuous, but smaller and often deformed. The separate teleuto-sori are

formed on other leaves on a localised mycelium, cause no deformation and are not conspicuous; in them are a few secondary uredospores. The telentospores have unusually coarse warts, mostly towards the apex, or are sometimes nearly or partially smooth. Bubák records (Centralbl. f. Bakter. 2. xvi. 158) that in many trials in three years he could never get the telentospores to germinate, and could not artificially produce infection in *Alchemilla*, though Klebahn (Zeitschr. f. Pflanzenkr. 1907) did so readily with the uredospores. This species can be gathered at considerable altitudes in Wales and Scotland (and as high as 7200 ft. in Switzerland).

DISTRIBUTION: Europe, Asia Minor, Greenland.

20. *Uromyces Ficariae* Lév.

Uredo Ficariae Schum. Pl. Säll. ii. 232.

Uromyces Ficariae Lév. Ann. Sci. Nat. 3. viii. 390. Cooke, Handb. p. 518; Micr. Fung. p. 212, pl. 7, f. 156—7. Plowr. Ured. p. 140. Sacc. Syll. vii. 568. Sydow, Monogr. ii. 208. Fischer, Ured. Schweiz, p. 13, f. 12.

Telentospores. Sori amphigenous or on the petioles, about $\frac{1}{2}$ mm. diam., rounded, frequently collected into dense orbicular or elongated clusters, on pale-yellow spots, especially on the petioles where they cause notable distortion, soon naked, pulverulent, chocolate-brown; spores more or less obovate, often irregular, not thickened above, but with a conical hyaline papilla, smooth, pale-brown, $22-38 \times 18-26 \mu$; pedicels hyaline, deciduous; a few subglobose, pale-brownish, faintly echinulate uredospores, each with three germ-pores, are occasionally found intermixed, but are usually abortive.

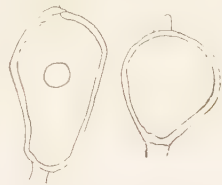


Fig. 60. *U. Ficariae*.
Telentospores, on *R.*
Ficaria.

On *Ranunculus Ficaria*. March to early June. Very common. (Fig. 60; see also Fig. 79.)

The æcidium on the same host belongs to the life-cycle of *Uromyces Poae*, and is considered to have no connection with the *Uromyces* on *R. Ficaria*, though it may be found on the same leaf. Klebahn proved that the telentospores reproduce themselves. But there is a curious conclusion arrived at by Tranzschel, as the result of his experiments

(see Bot. Zeit. lxiii. 75), that an æcidium which he finds on *R. Ficaria* is connected with *U. Rumicis* (q.v.). The spores of *U. Ficariae* and *U. Rumicis* are very similar.

DISTRIBUTION: Europe generally, except the extreme South.

21. *Uromyces caryophyllinus* Wint.

Lycoperdon caryophyllum Schrank, Baier. Flor. ii. 668.

Uromyces caryophyllinus Winter, Pilze, p. 149. Sacc. Syll. vii. 545.

Sydow, Monogr. ii. 210, 362. Fischer, Ured. Schweiz, p. 11, f. 10.

Trans. Brit. Myc. Soc. iii. 122. McAlpine, Rusts of Australia, p. 102, f. 152—4 and pl. G, f. 30—1.

Nigredo caryophyllina Arthur, N. Amer. Fl. vii. 246.

Uredospores. Sori amphigenous or on the stems, sometimes on pallid spots, scattered, minute, round or oblong, soon naked, pulverulent, cinnamon; spores globose to ellipsoid, sparsely echinulate, yellowish-brown, $20-35 \times 18-25 \mu$; epispore $2\frac{1}{2}-3 \mu$ thick, with three to five germ-pores.



Fig. 61. *U. caryophyllinus*. Teliospores and uredospore from the same sorus, on carnation; leaf of carnation with two groups of sori.

Teliospores. Sori confluent and large, mostly oblong, surrounded and often covered by the cleft epidermis, subpulverulent, brownish-black; spores globose to ellipsoid, with

a flat hyaline papilla, densely and minutely punctate, chestnut-brown, $20-31 \times 18-24 \mu$; epispore $2-3 \mu$ thick, not thickened at the summit; pedicels short, hyaline, deciduous.

On *Dianthus barbatus*, *D. Caryophyllus*, *D. chinensis*. On cultivated carnations practically all the year round. (Fig. 61.)

The "Carnation Rust" was introduced into England on imported plants about the year 1890; it sometimes occurs as an epidemic, causing much injury. The teleutospore-containing sori are often clustered on the leaves and stems in circinate or elongated swollen patches; uredospores are mixed with them. The punctuation of the teleutospores is perceptible only when they are viewed dry, and at the best is very indistinct.

It is stated by Tranzschel and Fischer that this species is heterœcious, and has its æcidium on *Euphorbia Gerardiana*, but as this *Euphorbia* does not occur in Britain, the parasite probably maintains itself here without heterœcism. It is remarked by Sydow that the same is true in Switzerland, at least in certain cases; but see Fischer (p. 530) who produced the fungus, from an æcidium on *E. Gerardiana*, on *Saponaria ocymoides*, but not on *Dianthus*. The fungus has now spread round the world in greenhouses, but only in the sporophytic stage; the æcidium has not been recognised anywhere except in Europe. The best means of prevention are (1) the selection of resistant varieties, (2) good and careful cultivation, especially sufficient ventilation. If spraying is resorted to, potassium sulphide solution ($\frac{1}{2}$ oz. to 1 gallon) is perhaps the best, but dilute Bordeaux mixture or copper sulphate solution (1 lb. to 50 gallons), or sponging with a rose-red solution of permanganate of potash have also been tried. The latter can be used even when the plants are in active growth. Besides spraying, every infected leaf should be plucked off and burnt as soon as discovered. This disease must not be confounded with the outwardly similar "Fairy Ring of Carnations," caused by *Heterosporium*, but the same remedies apply to both.

DISTRIBUTION: Europe, Western Asia, Japan, South Africa, North America, Australia.

22. *Uromyces Behenis* Unger.

Æcidium Behenis DC. Encycl. viii. 239. Cooke, Handb. p. 541; Micr. Fung. p. 197.

Uromyces Behenis Unger, Einfluss d. Bod. p. 216. Cooke, Micr. Fung. p. 213. Plowr. Ured. p. 138. Sacc. Syll. vii. 559. Sydow, Monogr. ii. 218. Fischer, Ured. Schweiz, p. 64, f. 48.

Æcidiospores. *Æcidia* usually hypophyllous, seated on spots that vary both in size and colour (yellow or purple) and are generally very conspicuous, solitary or collected into

clusters, cup-shaped, whitish-yellow, with a torn revolute margin; spores densely and minutely verruculose, yellowish, $15-21\ \mu$ diam.

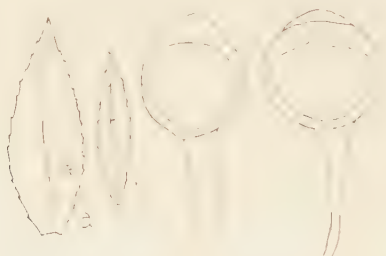


Fig. 62. *U. Behenii*. *a*, æcidia on early leaf, *b*, æcidia on later leaf, of *S. inflata*; two teleutospores.

Teleutospores. Sori hypophyllous and on the stems, often surrounding the secondary æcidia, irregularly scattered, gregarious or circinate, rounded or oblong, covered for a considerable time by the lead-coloured epidermis, rather small and compact, brownish-black or black; spores subglobose or obovate, rounded above and thickened (as much as $11\ \mu$), smooth, pale brown, $25-35 \times 20-27\ \mu$; pedicels persistent, faintly yellow, thick, as much as $75\ \mu$ long.

On *Silene inflata* (*latifolia*), *S. maritima*. Not common. Æcidia and teleutospores, July—October. (Fig. 62.)

The spots occupied by the æcidia vary in colour, but the primary ones are often tinged or margined with purple. This is one of the species whose æcidiospores are capable of reproducing the æcidia, as Dietel has shown (*Flora*, lxxi. 395, 1895). The primary æcidia, on the earlier leaves, are in roundish groups or concentric circles, only a few being scattered. The secondary æcidia, on the younger leaves, stand more often singly and are spread over a larger area; the teleuto-sori spring from the same secondary mycelium or are formed separately. The secondary æcidia are not confined to the beginning of the season, but continue to be produced till the end of autumn, being in fact the representatives of the uredo-sori.

On this account this species is very interesting biologically. The primary æcidia arise from infection by comparatively few basidiospores; the secondary arise from the more widely dispersed æcidiospores of the

first generation, and their mycelium can produce either æcidiospores or teleutospores or both. No spermogones seem to be known.

The æcidium requires to be carefully distinguished from that of *Puccinia Behenis* (*P. Silenes*) (q.v.), which is much rarer and does not extend throughout the season.

DISTRIBUTION: Europe generally.

23. *Uromyces sparsus* Lév.

Uromyces sparsus Lév. Ann. Sci. Nat. ser. 3, viii. 369. Cooke, Handb. p. 519; Micr. Fung. p. 214. Plowr. Ured. p. 136. Sacc. Syll. vii. 545. Sydow, Monogr. ii. 221.

Uredospores. Sori amphigenous and on the stems, on pallid spots, scattered, roundish, $\frac{1}{2}$ —1 mm. diam., convex, covered for a considerable time by the epidermis, which at length splits and surrounds them, then pulverulent, pallid-cinnamon; spores globose to oblong, faintly echinulate, brownish, $18\text{--}28 \times 15\text{--}22 \mu$.

Teleutospores. Sori similar, but darker; spores subglobose to oblong, rounded above where they are slightly thickened (up to 4μ) and darker, generally tapering downwards, smooth, brown, $22\text{--}32 \times 14\text{--}21 \mu$; pedicels persistent, thick, as much as 60μ long, brownish at the apex.



Fig. 63. *U. sparsus*.
Teleutospores on
Spergularia salina
(foreign, J. Kunze,
Exsicc., no. 216)

On *Spergularia rubra* (*Alsine rubra*). May July. Very rare; I have seen no British specimens. (Fig. 63.)

DISTRIBUTION: Mid-western Europe.

24. *Uromyces Chenopodii* Schröt.

Uredo Chenopodii Duby, Bot. Gall. ii. 899.

Æcidium Suaedae Thüm. Fung. Ægypt. iii. no. 53.

Æcidium Chenopodii, in Gard. Chron. (1895), xviii. 135.

Uromyces Chenopodii Schröt. in Kunz. Fung. Sel. no. 214. Plowright in Trans. Brit. Myc. Soc. i. 56. Sacc. Syll. vii. 548. Sydow, Monogr. ii. 233.

Æcidiospores. *Æcidia* amphigenous, clustered in circles 5—10 mm. diam., cylindrical, whitish, margin deeply torn; spores delicately verruculose, yellow, 18—22 μ diam.

Uredospores. Sori amphigenous, scattered or gregarious, round or more frequently elongate, small, surrounded by the conspicuous torn epidermis, cinnamon; spores globose to oval or oblong, delicately and sparingly echinulate, yellowish-brown, 18—25 $\times$ 16—21 μ ; episporium about 1½ μ thick.

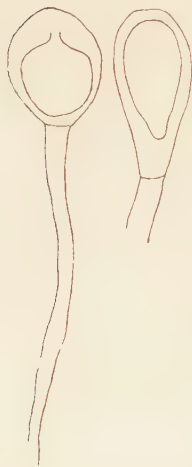


Fig. 64. *U. Chenopodii*.
Teleutospores on
Suaeda fruticosa
(foreign, ex herb. De
Thümen).

Teleutospores. Sori amphigenous but mostly cauline, on the leaves rounded and 1—3 mm. diam., on the stems lanceolate and even as much as 3 cm. long (Sydow), thick, compact, dark-brown; spores very variable, oval to subpyriform, rounded or subconical at the apex, thickened or not, smooth, brown, 24—35 $\times$ 18—20 μ ; pedicels pale-brown, persistent, up to 80 μ long or more.

On stems, branches and leaves of *Suaeda maritima*. Rare. Terrington Marsh (Mr H. G. Ward); North Wootton Marsh (C. B. P.); August. The *æcidia* are recorded from Worthing (Miss A. L. Smith, Journ. of Bot. May, 1898), as well as by Plowright from North Wootton. (Fig. 64.)

Teleutospores very variable, short and broad or long and narrow in the same sorus; thickening of apex also varying from 3 to 7 μ ; pedicels often very long and flexuous.

The name of this species is misleading; it has been found on *S. fruticosa*, but not on the present-day *Chenopodium*. Plowright mentions, as showing the distinctness of this species from *U. Salicorniae*, that at North Wootton Marsh it did not spread to *Salicornia herbacea*, which was growing near.

DISTRIBUTION: Germany, and most of the countries in South Europe and North Africa.

25. **Uromyces Betae** Lév.

Uredo Betae Pers. Syn. p. 220.

Trichobasis Betae Cooke, Handb. p. 530; Micr. Fung. p. 225.

Uromyces Betae Lév. Ann. Sci. Nat. ser. 3, viii. 375. Cooke, Micr. Fung. p. 213. Plowr. Ured. p. 127. Sacc. Syll. vii. 536. Sydow, Monogr. ii. 224. Fischer, Ured. Schweiz, p. 10, f. 9. McAlpine, Rusts of Australia, p. 100, f. 148—9, 316, and pl. H.

Nigredo Betae Arthur, N. Amer. Fl. vii. 245.

Spermogones. In little clusters, honey-coloured.

Æcidiospores. Æcidia amphigenous, often on rounded or irregular yellowish spots, collected into rather large clusters which are round or sometimes irregular and confluent, cup-shaped, yellowish, with a reflexed incised margin; spores delicately verruculose, pale-yellowish, $16\text{--}24 \times 16\text{--}20 \mu$.

Uredospores. Sori amphigenous, scattered, sometimes concentrically arranged, thick, pulvinate, circular, up to 2 mm. diam., covered by the epidermis which at length splits, then pulverulent, cinnamon; spores globose to obovate-oblong, sparsely and minutely echinulate, yellowish, $21\text{--}32 \times 16\text{--}26 \mu$; epispore $2\frac{1}{2}\text{--}3 \mu$ thick, with two equatorial germ-pores.



Fig. 65. *U. Betae*. Teleutospore and uredospore, on *B. maritima*.

Teleutospores. Sori similar, but somewhat compact, dark-brown; spores globose to obovate, rounded and slightly thickened above, with a minute hyaline hemispherical papilla, smooth, pale-brown, $22\text{--}34 \times 18\text{--}25 \mu$; pedicels short, hyaline.

On leaves of *Beta maritima*, *B. vulgaris*; also doing great harm to cultivated mangels. Æcidia rather rare, April—June; uredo- and teleutospores, rather common, May—October. (Fig. 65.)

In May all four spore-forms can sometimes be seen on the same leaf. Kühn says that the mycelium of the æcidia is perennial, and that its spores can reproduce the æcidia. If possible, the first leaves seen bearing the æcidia should be collected and burnt; this will check the disease at the outset. If this is not possible, the plants may be sprayed with dilute Bordeaux mixture or with potassium sulphide solution. Since in mangels the disease would chiefly be reproduced by teleutospores from old leaves

of the preceding crop, all affected mangel "tops" should be burnt: rotation of crops is of course a sure preventive, as in all such cases.

DISTRIBUTION: Europe, California, South Africa, Australia, New Zealand.

26. *Uromyces Salicorniæ* De Bary.

Æcidium Salicorniæ DC. Flor. fr. vi. 92.

Uromyces Salicorniæ De Bary, in Rab. Fung. Eur. nos. 1385—6.

Cooke, Grevillea, vii. 137. Plowr. Ured. p. 129. Sacc. Syll. vii. 538. Sydow, Monogr. ii. 230.

Æcidiospores. *Æcidia* on the cotyledons chiefly, scattered or in small clusters, at first hemispherical, then cup-shaped, with erect, torn, white margin; spores finely verruculose, orange-yellow, 17—35 μ .

Uredospores. Sori scattered or aggregated, minute, rounded, long covered by the epidermis, pulverulent, cinnamon; spores ovate to pyriform, very finely echinulate, yellow-brown, 24—35 $\times$ 18—25 μ ; episore about 1½ μ thick.

Teleutospores. Sori similar, but larger and rather compact, dark-brown; spores subglobose to obovate, rounded above and often thickened (up to 4 μ), and surmounted by a thin, broad, dark cap, rounded below, smooth, brown, 25—35 $\times$ 18—28 μ ; pedicels hyaline, thick, persistent, as much as 80 μ long.

Fig. 66. *U. Salicorniæ*. Teleutospores on *S. herbacea*.

On leaves and stems of *Salicornia europæa* (*herbacea*). October — November. Rare. (Fig. 66.)

The teleuto-sori are chiefly on the stems, as much as 3 mm. long, and very pulvinate.

DISTRIBUTION: France, Germany.

27. *Uromyces Rumicis* Wint.

Uredo Rumicis Schum. Pl. Säll. ii. 231.

Trichobasis Rumicum DC.; Cooke, Micr. Fung. p. 225 p.p.

Uromyces apiculosa Lév.; Cooke, Handb. p. 518; Micr. Fung. p. 212 p.p. (excl. figs.).

U. Rumicis Wint. Krypt. Fl. i. 145. Plowr. Ured. p. 135 p.p. Sacc. Syll. vii. 544. Sydow, Monogr. ii. 238. Fischer, Ured. Schweiz, p. 9, f. 8.

Uredospores. Sori amphigenous, on coloured spots, round, minute, scattered, soon naked, pulverulent, cinnamon; spores subglobose to ellipsoid, sparsely echinulate, pale-brown, $20-28 \times 18-24 \mu$, with two (more often three) germ-pores.

Teleutospores. Sori similar, but darker; spores subglobose to pyriform, with a hemispherical hyaline papilla, often narrowed below, smooth or nearly so, brown, $24-35 \times 18-24 \mu$; episporium rather thick; pedicels thin, hyaline, deciduous.



Fig. 67. *U. Rumicis*. Teleutospores and uredospore, on *R. obtusifolius*.

On *Rumex conglomeratus*, *R. crispus*, *R. Hydrolapathum*, *R. nemorosus*, *R. obtusifolius*, and perhaps others. May—September. Common. (Fig. 67.)

The spots on the leaves are small, round, and of various colours; often the chlorenchyma in the immediate neighbourhood retains its green colour long after the rest of the leaf has become faded and yellow.

It will be noticed that the spores of *U. Rumicis* are exactly like those of *U. Ficariae*, and for this reason Tranzschel was led to suspect some connection between the two, such as he demonstrated to exist between *P. fusca* and *P. Pruni-spinosae*, whose teleutospores are equally alike. In 1905 he reported that he had produced an æcidium on *Ranunculus Ficaria* from the spores of *U. Rumicis*; still later, he repeated this statement (1909), and added that he had infected *Rumex obtusifolius* with æcidiospores from *R. Ficaria*. Other experimenters (Bubák, Krieg), have been unable to repeat the former of these infections; they could only produce the æcidium on *R. Ficaria* with the spores of *Uromyces Poea*. It has been suggested that there are two æcidia on *R. Ficaria*, one belonging to *U. Poea* and the other to *U. Rumicis*; I have tried to infect *R. obtusifolius* with æcidiospores from *R. Ficaria*, brought from a place where the æcidium on it and the *Uromyces* on *R. obtusifolius* were both very abundant, but the attempt failed. Krieg (Centralbl. f. Bakt. 1906), obtained uredospores on *R. Acetosa* with æcidiospores from *R. Ficaria*, but the same material infected species of *Poa* (especially *P. trivialis*), and the possibility

of contamination by foreign spores was not entirely excluded in his experiments. Judgment on this point must be suspended.

DISTRIBUTION: Europe, Algeria, Asia Minor, Africa, California, Chili.

28. *Uromyces Acetosæ* Schröt.

Uredo bifrons DC. ; Cooke, Handb. p. 528 ; Micr. Fung. p. 217, pl. vii. figs. 137—9.

Uromyces Rumicis Wint. ; Plowr. Ured. p. 135 p.p. Fischer, Ured. Schweiz, p. 9 (not f. 8) p.p.

U. Acetosæ Schröt. in Rab. Fung. Europ. no. 2080 (1876). Sacc. Syll. vii. 537. Sydow, Monogr. ii. 241.

[*Spermogones*. Honey-coloured, clustered.

Æcidiospores. *Æcidia* amphigenous or on the petioles, in dense clusters (up to 1 cm. broad), cup-shaped, whitish-yellow, with a cut and revolute margin; spores nearly smooth or very minutely punctate, clear-yellowish, $18-21 \times 12-18 \mu$.]

Fig. 68. *U. Acetosæ*.
Teleutospores, on
R. Acetosa.

Uredospores. Sori amphigenous, often seated on red or purple spots, scattered or circinate, minute, pulverulent, cinnamon; spores subglobose to ellipsoid, finely and densely verruculose, yellowish or pale brownish-yellow, $18-25 \times 17-22 \mu$; epispore about $2\frac{1}{2} \mu$ thick, with three germ-pores.

Teleutospores. Sori similar, but dark-brown; spores subglobose to ellipsoid, not thickened above, or rarely with a paler and very minute papilla, rounded below, beset with very minute warts arranged in lines, brown, $21-26 \times 20-24 \mu$; epispore rather thick; pedicels thin, hyaline, deciduous.

On leaves and petioles of *Rumex Acetosa*, *R. Acetosella*. May—September. Not uncommon. (Fig. 68.)

Allied to *U. Rumicis*, but *U. Acetosæ* has shorter spores (of both kinds) and the hyaline papilla of the teleutospores is almost always wanting. The *æcidium* has not been found in Britain, but the other stages are rather common: the uredo- and teleutospores are unusually alike, but can be distinguished by the germ-pores and the fewer warts of the latter.

On the same host-plants is a *Puccinia*, which (in the absence of the teleutospores) can be distinguished only by the fact that the uredospores have two (rarely three) germ-pores and are adorned with few and distant spines. There is little doubt that many of the specimens recorded as *U. Acetosae* are really the uredospores of *Puccinia Acetosae*.

DISTRIBUTION : Germany, France, Sweden, Norway, Finland.

29. *Uromyces Polygoni* Fekl.

Æcidium aviculariae Kze. ; Cooke, Handb. p. 545 ; Micr. Fung. p. 199.

Puccinia vaginalium Link ; Cooke, Handb. p. 495 ; Micr. Fung. p. 204.

Trichobasis Polygonorum Berk. ; Cooke, Micr. Fung. p. 226 p.p.

Uromyces Polygoni Fekl. Symb. Myc. p. 64. Cooke, Handb. p. 519 ;

Micr. Fung. p. 213. Plowr. Ured. p. 123. Sacc. Syll. vii. 533.

Sydow, Monogr. ii. 236. Fischer, Ured. Schweiz, p. 61, f. 46.

McAlpine, Rusts of Australia, p. 99, f. 150—1.

Spermogones. Honey-coloured, conical, only a few together.

Æcidiospores. Mostly hypophyllous, on yellow or violet spots, irregularly aggregated or in circular groups, cup-shaped, whitish, with a cleft and revolute margin ; spores verruculose, yellowish, $15-21 \times 14-18 \mu$.

Uredospores. Sori amphigenous or on the stems, scattered or in small clusters, small, round, soon naked, pulverulent, cinnamon ; spores globose to ellipsoid, densely and minutely verruculose, pale-brown, $18-26 \times 17-24 \mu$; episporium $1\frac{1}{2}-2\frac{1}{2} \mu$ thick, with three or four germ-pores.

Teleutospores. Sori like the uredosori, but larger and more confluent upon the stems, compact, dark-brown ; spores globose or obovate, rounded above and thickened (up to 6μ), smooth, chestnut-brown, $22-38 \times 14-22 \mu$; pedicels coloured, persistent, thick, as much as 90μ long.

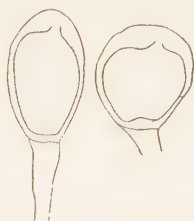


Fig. 69. *U. Polygoni*.
Teleutospores, on *P. aviculare*.

On *Polygonum aviculare*. *Æcidia*, rare, May—June, Manchester (T. Brittain), 1875 ; uredo- and teleutospores, very common, July—November. (Fig. 69.)

The connection of the æcidium with the later stages seems not yet to have been experimentally demonstrated: but McAlpine found the æcidia on young plants of *P. aviculare* along with the other spore-forms. In Europe, etc. it is recorded on many other species of *Polygonum*.

This species is said to occur also on *Rumex Acetosella* on the continent, and should be looked for here on that host. If so, there would be three species on *R. Acetosella* to be considered: *U. Polygoni* which has verruculose uredospores and smooth teleutospores; *U. Acetosae* which is distinguished by having teleutospores beset with a few minute warts arranged in lines; while *Puccinia Acetosae* has aculeolate uredospores and teleutospores with many delicate warts.

DISTRIBUTION: World-wide.

30. *Uromyces Lilii* Fekl.

Caeoma Lilii Link, Sp. Pl., ii. 8.

Uromyces Lilii Fekl. Symb. Myc. Nachtr. iii. 16. Sydow, Monogr. ii. 277. Fischer, Ured. Schweiz, p. 6, f. 5. Grove, Journ. Bot. 1911, p. 368.

U. Erythronii DC. ; Sacc. Syll. vii. 564 p.p. Wild Fauna and Flora of Kew, p. 163 (non *U. Erythronii* Pass.?).

Nigredo Lilii Arthur, N. Amer. Fl. vii. 242.

Spermogones. Dispersed among the æcidia, brownish-yellow.

Æcidiospores. Æcidia amphigenous, usually hypophyllous, or even on the petioles and stems, seated on lanceolate yellowish spots, in rounded or elongated groups of very different sizes, and often extending widely, more or less crowded, for a long time hemispherical and closed, at length opening by a central pore, but scarcely cup-shaped, margin not revolute, about $\frac{1}{2}$ mm. diam. yellow; spores densely and minutely verruculose, yellowish, $22-35 \times 18-26 \mu$; epispore 3μ thick or less.

Teleutospores. Sori amphigenous, usually hypophyllous, on large yellowish spots, scattered or collected in groups, rounded or oblong, elongated on the petioles, at first covered by the epidermis, which at length splits, large, pulverulent, dark-brown; spores globose to oblong or pyriform, rounded above, with a prominent hyaline papilla, covered when mature with short ridges which are often disposed in lines more or less

interrupted and anastomosing, brown, $28-44 \times 22-30 \mu$; epispore $2-3\frac{1}{2} \mu$ thick; pedicels hyaline, slender, deciduous.

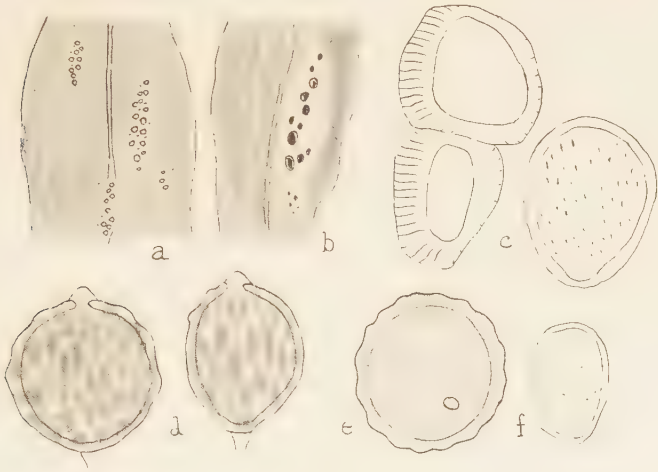


Fig. 70. *U. Lilii*. *a*, leaf of *Lilium candidum*, with æidia; *b*, another, with teleuto-sori, nat. size; *c*, cells of peridium, in section and inner face-view; *d*, teleutospores; *e*, teleutospore seen from above; *f*, æcidiospore, all $\times 600$.

On *Lilium candidum*. Kew Gardens; also at Birmingham, 1911-3 (C. W. Lowe). Æidia in April, May; mature teleutospores from June. (Fig. 70.)

The part of the leaf occupied by the æidia is somewhat thickened, and the æidia scarcely protrude above the epidermis. The peridia are slow in opening. The streaked teleutospores are very distinctive. The lilies on which the parasite appeared at Birmingham had been in the garden for some years, but it was not noticed till 1911. Fischer records it on *Fritillaria Meleagris*, and Sydow and Arthur on other species of the two genera. The true *U. Erythronii* differs from this species in possessing a truly cup-shaped æcidium with a distinctly revolute margin. But the teleutospores of the Birmingham specimens were more like those figured by Fischer under *U. Erythronii* than those which he figures on *Fritillaria Meleagris* (f. 5), though devoid of the "Queranastomosen." Possibly the species on *Lilium* is quite distinct from that on *Fritillaria*. The longitudinal striæ are so plainly marked as to be visible under a comparatively low power. As Fischer remarks, the cells of the lower part of the peridium are much thinner-walled than those in the upper part.

DISTRIBUTION: Central Europe, North America.

31. **Uromyces Gageæ** Beck.

Uromyces Gageæ Beck, Verh. k.-k. zool.-bot. Gesell. Wien, xxx. 26.
Sacc. Syll. vii. 568. Sydow, Monogr. ii. 273. Fischer, Ured.
Schweiz, p. 4, f. 3.

U. Ornithogali Plowr. Ured. p. 142.

Teleutospores. Sori amphigenous, scattered, roundish or elliptical, 1—3 mm. long, covered by the lead-coloured epidermis which at length splits longitudinally, then naked, pulverulent, dark-brown; spores subglobose to obovoid, not or scarcely thickened above, but usually with a hyaline apiculus, smooth, brown, $26\text{--}40 \times 18\text{--}28 \mu$; epispore 2μ thick; pedicels hyaline, shorter



Fig. 71. *U. Gageæ*.
Teleutospores.

than the spores.

On leaves of *Gagea lutea*. Rare. April, May. (Fig. 71.)

The teleutospores mature in spring, according to Fischer. Plowright says that the mycelium causes variously shaped pale spots on the affected leaves; but I find no spots and in Sydow it is said that there are none.

DISTRIBUTION: Western and Central Europe.

32. **Uromyces Scillarum** Wint.

Uredo Scillarum Grev. in Smith, Engl. Fl. v. 376.

Uromyces concentricus Lev.; Cooke, Handb. p. 519; Greville, vii. 138;
Micr. Fung. p. 213.

U. Scillarum Winter, Pilze Deutschl. p. 142; Plowr. Ured. p. 141.
Sacc. Syll. vii. 567. Sydow, Monogr. ii. 278. Fischer, Ured.
Schweiz, p. 2, f. 1.

Teleutospores. Sori amphigenous, usually seated on pallid or yellowish spots, small, round or oblong, up to $\frac{1}{2}$ mm. diam., collected into round or oblong clusters, often concentrically arranged, sometimes confluent, long covered by the epidermis which at length splits and surrounds them, pulverulent, dark-brown; spores subglobose to oblong, usually rounded and not thickened



Fig. 72. *U. Scillarum*. Teleutospores, on *S. nutans*; a, teleutospore, on *S. campanulata*.

above, smooth, occasionally marked with a few very faint lines

running from apex to base, evenly coloured, brown, $18-32 \times 14-22 \mu$; epispore uniformly thin, about $1\frac{1}{2} \mu$ thick; pedicels hyaline, often deciduous, as long as or longer than the spore.

On leaves of *Eudymion non-scriptum* (*Scilla nutans*), and also of *Scilla bifolia*, *S. campanulata*. Common. April—June. (Fig. 72.)

The yellow spots and the concentric arrangement of the sori are often very marked. The mycelium is purely local. A few finely echinulate uredospores, $27 \times 20 \mu$, were found by Juel in the young sori on *Scilla obtusifolia* (Bull. Soc. Myc. Fr. xvii. 259).

DISTRIBUTION: Central and Southern Europe and Morocco.

33. *Uromyces ambiguus* Lév.

Uredo ambigua DC. Flor. fr. vi. 64.

U. Alliorum Cooke, Handb. p. 528; Micr. Fung. p. 217 p.p.

Puccinia mixta Fekl., forma *simplicior* Körn.

Uromyces Alliorum DC.; Cooke, Handb. p. 518; Micr. Fung. p. 212.

Plowr. Ured. p. 137 p.p.

U. ambiguus Lév. Ann. Sci. Nat. 3, viii. 375. Sacc. Syll. vii. 543.

Sydow, Monogr. ii. 262. Grove, Journ. Bot. 1911, p. 367.

Uredospores. Sori amphigenous, without spots, scattered, roundish or oblong, long covered by the epidermis, yellowish; spores globose to obovate, delicately verruculose, pale-yellowish, $20-28 \times 17-22 \mu$; epispore $3-3\frac{1}{2} \mu$ thick, with six or seven germ-pores.

Teleutospores. Sori amphigenous and on the stems, on the leaves scattered, small and roundish, on the stems confluent and larger, up to 15 mm. long, always covered by the blue-grey epidermis; spores subglobose to pyriform, rounded above, without a papilla and scarcely thickened, rounded or narrowed below, smooth, brown, $20-35 \times 17-24 \mu$; pedicels thin, hyaline, fragile, as much as 30μ long.



Fig. 73. *U. ambiguus*. Teleutospores and uredospore on *Allium Scorodoprasum*.

On *Allium Schoenoprasum*, *A. Scorodoprasum*, and (according to Sydow) *A. sphaerocephalum*. Not common. (Fig. 73.)

It cannot be considered as certain that this is a species distinct from *Puccinia Porri* Wint., but as it presents slight differences, it is better, in the total absence of culture experiments, to keep it separate for the time. The difficulty lies in the fact that the teleutospores of this *Uromyces* agree perfectly with the mesospores of the *Puccinia* (except perhaps in the greater variability of the latter); but the teleutospores of the *Uromyces* are generally larger and more persistently covered by the epidermis, and one searches in vain in them for *two-celled* spores, such as are found freely in the sori of the *Puccinia*. Fischer says that the uredospores of *P. Porri* have only three germ-pores. According to Sydow, the *Uromyces* occurs only on the three species of *Allium* mentioned above and *A. rotundum*, while the *Puccinia* is found on them as well as on many other species of the genus. Nevertheless the two forms are closely allied and from the evolutionary point of view the *Uromyces* must be regarded as a specialised state or mutation of the *Puccinia*. Neither of them has an aecidial stage.

DISTRIBUTION: Central and North-Western Europe.

34. *Uromyces Colchici* Massee.

U. Colchici Mass. Grevillea, xxi. 6, pl. 182, f. 16—18; Diseases of Cult. Plants, p. 292, f. 85; Text-book of Plant Diseases, p. 227, f. 56. Sydow, Monogr. ii. 268.

Teleutospores. Sori amphigenous, scattered, rather large, elliptical, sometimes circinating, up to 2 mm. long, covered for some time by the epidermis which at length splits, then sub pulverulent, brown; spores subglobose to ovate, rounded above, with a broad flat hyaline papilla, smooth, pale-brown, $28-40 \times 20-28 \mu$; episporium $3-3\frac{1}{2} \mu$ thick; pedicels hyaline, rather long, but very deciduous.



Fig. 74. *U. Colchici*. Teleutospore, from the original specimen.

On leaves of *Colchicum speciosum*. Kew Gardens; unknown in the world elsewhere. (Fig. 74.)

The teleutospores remain on the dead leaves and germinate in the following spring, so that if *Colchicum* is again planted in the same ground or allowed to remain there, it is liable to contract the disease year after year. As in all similar cases, the best preventive against future attacks

is to remove carefully and burn all diseased leaves before they mature their spores.

The fungus is stated to have attacked the foliage of the host for three successive seasons, completely destroying it, and although for the first two seasons it did not attack other species of *Colchicum* growing near, during the third season it spread to *C. autumnale* and *C. bavaricum*.

35. *Uromyces Junci* Tul.

Æcidium zonale Duby, Bot. Gall. ii. 906. Cooke, Grevillea, xiv. 39.

Uromyces Junci Tul. Ann. Sci. Nat. ser. 4, ii. 146. Cooke, Grevillea, vii. 139; Micr. Fung. p. 213. Plowr. Ured. p. 132; Grevillea, xi. 52. Sacc. Syll. vii. 541. Sydow, Monogr. ii. 287. Fischer, Ured. Schweiz, p. 57, f. 43.

Nigredo Junci Arthur, N. Amer. Fl. vii. 238.

Spermogones. Usually epiphyllous.

Æcidiospores. *Æcidia* hypophyllous, seated on spots which are zoned with yellow and purple, in dense circinate clusters 2—5 mm. wide, cup-shaped, yellowish-white, with a torn revolute margin; spores densely and minutely verruculose, transparent-yellowish, 17—21 μ .

Uredospores. Sori scattered, roundish or oblong, up to 1 mm. long, surrounded by the cleft epidermis, pulverulent, brown; spores globose to ellipsoid, faintly echinulate, yellowish-brown, 20—28 $\times$ 16—22 μ , with two equatorial germ-pores.

Teleutospores. Sori amphigenous or on the culms, scattered or occasionally aggregated, similar to the uredo-sori, but darker; spores oblong-ovate to clavate, rounded or conical above and much thickened (up to 14 μ), attenuated below, smooth, dark-brown, 24—42 $\times$ 12—18 μ ; pedicels thick, persistent, brownish, as much as 60 μ long.

Æcidia on *Pulicaria dysenterica*, May—July; uredo- and teleutospores on *Juncus obtusiflorus*, from July onwards, lasting through the winter on the dead culms. Not common. (Fig. 75.)



Fig. 75. *U. Junci*. Teleutospores, on *J. obtusiflorus*.

The connection of the two forms, first proved by Fuckel and Plowright, has been confirmed by Fischer. On the continent and elsewhere, there are forms of *Uromyces* on other species of *Juncus*, some of which (and possibly most of them) have their æcidia on other hosts than *P. dysenterica*.

DISTRIBUTION: Central and Western Europe, Algeria, North and South America.

36. *Uromyces Scirpi* Burr.

Æcidium Glaucis D. et M. ; Cooke, Grevillea, xv. 29; Plowr. Ured. p. 268 ; Gard. Chron. ser. 3, vii. 682, 746.

Uredo Scirpi Cast. Catal. Pl. Marseille, p. 214.

Uromyces Scirpi Burr. Parasit. Fung. Illinois, p. 168. Sacc. Syll. vii. 558. Sydow, Monogr. ii. 302.

U. lineolatus Desm. ; Plowr. Grevillea, xxi. 111.

U. maritimae Plowr. Gard. Chron. ser. 3, vii. 682, 746 ; Jour. Roy. Hort. Soc. (1890), p. cix. Klebahn, Wirtswechs. Rostpilze, p. 328.

Nigredo Scirpi Arthur, N. Amer. Fl. vii. 233.

Spermogones. Usually epiphyllous.

Æcidiospores. Æcidia hypophyllous or on the petioles, in rather small clusters, cup-shaped, with an incised revolute margin ; spores densely and minutely verruculose, transparent-yellowish, $16-24 \times 14-20 \mu$.

Uredospores. Sori hypophyllous, scattered or arranged in lines, rounded or oblong, up to 1 mm. long, surrounded by the cleft epidermis, pulverulent, cinnamon ; spores globose to ovate, distantly and minutely echinulate, yellowish-brown, $22-35 \times 16-25 \mu$; episore $1\frac{1}{2}-2 \mu$ thick, with three equatorial germ-pores.



Fig. 76. *U. Scirpi*.
Teliospores,
on *S. flaccidus*,
Illinois, U.S.A.

Teliospores. Sori amphigenous, on indefinite discoloured spots, scattered or confluent in lines, long covered by the epidermis, brownish-black ; spores oblong to clavate, tapering usually and thickened (up to 12μ) above, attenuated below, smooth, pale-brown, $26-45 \times 15-24 \mu$; pedicels brownish, persistent, as long as or longer than the spore.

Æcidia on leaves and petioles of *Glaux maritima*, May; uredo- and teleutospores on *Scirpus maritimus*, June to August. Banks of the Humber, Hull. (Fig. 76.)

The researches by which Plowright proved the connection of these two forms are given in Grevillea, xxi. 111, and in Journ. R. Hort. Soc. xii. p. cx.; other observers have found a similar *Uromyces* on *Scirpus maritimus* and therefrom have produced æcidia on other host plants such as *Pastinaca sativa* (Rostrup), *Berula angustifolia*, *Daucus Carota* (Bubák), *Ananthe aquatica* (Klebahn), *Hippuris vulgaris* and *Sium latifolium* (Dietel), etc. In North America, a morphologically indistinguishable *Uromyces* on *Scirpus fluviatilis*, etc. has produced an æcidium on *Cicuta maculata* (Arthur), and similar æcidia on allied Umbellifere are suspected to belong to the same life-cycle. It is evident that *U. Scirpi*, like *Puccinia Isiacae*, is in its æcidial stage a plurivorous species, though possibly some of these forms may be separated in the future as "biological" races. In any case, they are not so sharply distinguished as in other instances, but Klebahn isolates our British species as *U. maritimae* Plowr. See the full account in Sydow, Monogr. ii. pp. 304—7.

DISTRIBUTION: Europe and North America.

37. *Uromyces Dactylidis* Otth.

Æcidium Ranunculi-acris Pers. Obs. Myc. ii. 22.

Æ. Ranunculacearum DC. Fl. fr. vi. 97 p.p. Cooke, Handb. p. 539; Micr. Fung. p. 196 p.p.

Uromyces Dactylidis Otth, Mittheil. Nat. Gesell. Bern, 1861, p. 85.

Plowr. Ured. p. 130. Sacc. Syll. vii. 540 p.p. Sydow, Monogr. ii. 309. Fischer, Ured. Schweiz, p. 71, f. 54.

U. graminum Cooke, Handb. p. 520; Micr. Fung. p. 214.

Spermogones. Epiphyllous, honey-coloured, but also a few scattered among the æcidia on the lower surface.

Æcidiospores. Æcidia hypophyllous or on the petioles, seated on yellow spots, in roundish or, on the petioles, elongated clusters, cup-shaped, yellow, with slightly torn, recurved margin; spores delicately verruculose, pale-yellowish, 17—25 μ .

Uredospores. Sori amphigenous, scattered or in rows, small, elliptic or oblong, long covered by the epidermis, pulverulent, yellow-brown; spores globose to ovate, delicately echinulate, yellow or yellow-brown, 21—32 $\times$ 18—25 μ ; epispore 1½—2 μ thick, with 7—9 germ-pores; paraphyses generally wanting.

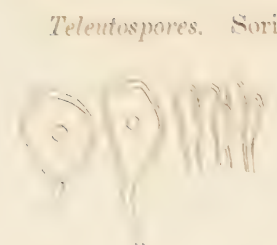


Fig. 77. *U. Dactylidis*. Teleutospores and the accompanying paraphyses.

Teleutospores. Sori generally hypophyllous, similar to the uredo-sori but more often confluent, always covered by the epidermis, compact, shining, black; spores ovate-oblong, occasionally ellipsoid or pyriform, rounded above, rarely truncate, often slightly thickened (up to 4μ), smooth, yellow-brown, darker only along the summit. $18-30 \times 14-20\mu$; epispore $1\frac{1}{2}\mu$ thick; pedicels brownish, persistent, nearly as long as the spore; paraphyses numerous, brown, agglutinated, dividing the sori into compartments.

Æcidia on *Ranunculus acris*, *R. bulbosus*, *R. repens*, March—May: uredo- and teleutospores on *Dactylis glomerata*, from July onwards, often covering the leaves, less often the sheaths and culms, and persisting through the winter, especially on the latter. (Fig. 77.)

This species and the following (*U. Poae*) are very closely allied, and should possibly be united. Perhaps more experimental cultures have been carried out with these two species than with most other Uredines; but the result is only a wild confusion of contradictory statements, from which one can infer, either that an immense number of intricately connected, but morphologically indistinguishable forms, inhabit the species of *Ranunculus* and of *Poa* and *Dactylis*—or, preferably, that the factors which govern the success of an attempted infection are so numerous and so little known, that failure does not afford any ground for arriving at a definite conclusion. Those who wish to learn further should consult the long account of these results given in Sydow, *Monographia*, ii. pp. 312—16.

In the British specimens of *U. Dactylidis* which I have examined, the paraphyses in the teleuto-sori, though often overlooked, are a conspicuous feature. But upon the question of paraphyses in the uredo-sori no agreement has been arrived at; the various authorities flatly contradict one another. Either, therefore, the paraphyses occur differently in different countries, as Plowright suggests, or more than one species is included under this title, or their presence or absence is a matter of no importance. Against the latter suggestion, however, we must set the fact that in other cases, e.g. in *Puccinia Sonchi*, the paraphyses form a constant and distinctive character.

An æcidium occurring on *Ranunculus acris* belongs to *Puccinia perplexi* Plowr., but cannot be distinguished from the present one,

except by cultures ; see also under *U. Poae*. The teleuto-sori of the present species are more numerous and much more conspicuous than those of *U. Poae*. They resemble the spots of *Phyllachora graminis* on the same host.

DISTRIBUTION : Europe only, not yet found in America.

38. **Uromyces Poæ** Raben.

Æcidium crassum var. β *Ficariae* Pers. ; Sow. pl. 397, f. 4.

Æ. Ranunculacearum DC. ; Cooke, Handb. p. 539 ; Micr. Fung. p. 196, pl. ii, figs. 12—14, p.p.

Uromyces Poæ Rab. Unio itin. 1866, no. 38. Plowr. Ured. p. 131. Sydow, Monogr. ii. 310. Fischer, Ured. Schweiz, p. 72, f. 55.

Spermogones. Epiphyllous, honey-coloured, a few also on the lower surface among the æcidia.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, in roundish clusters on yellow spots, which on the petioles are often elongated, cup-shaped, yellow, with torn, recurved margin ; spores delicately verruculose, clear-yellow, $17-25 \times 12-20 \mu$.

Uredospores. Sori amphigenous, scattered or in rows, small, elliptic or oblong, at first covered by the epidermis, pulverulent, yellowish-brown ; spores globose to ovate, faintly echinulate, yellow, $14-25 \times 14-20 \mu$; epispore $1\frac{1}{2}-2 \mu$ thick, with 4—9 germ-pores ; a few paraphyses occasionally intermixed.



Fig. 78. *U. Poæ*. Telentosporangia and the accompanying paraphyses, on *P. trivialis*.

Teleutospores. Sori generally hypophyllous, similar to the uredo-sori, but always covered by the epidermis, compact and black ; spores oblong-ellipsoid to pyriform, rounded or truncate above, not much thickened (up to 4 or 5μ), smooth, yellowish-brown, apex alone darker, $17-28 \times 14-20 \mu$; epispore $1\frac{1}{2} \mu$ thick ; pedicels brownish, as long as or shorter than the spore ; paraphyses numerous, brown, agglutinated, as in *U. Dactylidis*.

Æcidia on *Ranunculus auricomus*, *R. bulbosus*, *R. Ficaria*, *R. repens*, March—May ; uredo- and telentosporangia on *Poa annua*, *P. nemoralis*, *P. pratensis*, *P. trivialis*, May—September. (Fig. 78 ; see also Fig. 211.)

Concerning the difference between this species and *U. Dactylidis* (apart from the habitat) little that is definite can be said. Some authors unite them, but I find the teleutospores of *U. Poae* to be usually more oblong and often provided with shorter pedicels and the sori to be less conspicuous. The leaves of *Poa* are smaller than those of *Dactylis*, and the teleuto-sori do not cover them in such enormous numbers and never extend to the culms.

Juel divides this species into 9 or 10 biological races, but there is the usual conflict between different experimenters as to their limits. Some would even deny, what has been proved several times, that an æcidium on *R. Ficaria* belongs here: see *U. Rumicis* (p. 115). This æcidium and *U. Ficariae* may occasionally be found on the same leaf of *R. Ficaria*. (Fig. 79.)

Fig. 79. Æcidia of *U. Poae* (b) and teleutospores of *U. Ficariae* (a), on a leaf of *R. Ficaria*, nat. size.

It must not be forgotten that an æcidium which occurs on *R. bulbosus* and *R. repens* belongs to *Puccinia Magnusiana*: this is morphologically indistinguishable but is said to be later in its appearance. The æcidia which can be seen on *R. repens* in July and August possibly all belong to this latter species. The teleutospores of *U. Poae* can most easily be found by looking on the lower leaves of *Poa* in June or July, along a damp road-side where *R. repens* is abundant.

DISTRIBUTION: Europe, Asia Minor, Nova Scotia.

PUCCINIA Pers.

Autæcious or heteræcious.

Spermogones as in *Uromyces*. Æcidia with a peridium, which is occasionally evanescent; spores as in *Uromyces*. Uredospores as in *Uromyces*. Teleutospores two-celled, rarely one- or several-celled, the upper cell usually with an apical pore, less often the pore is displaced to the side; the lower cells with a pore just beneath the septum or rarely at a lower level. Basidiospores as in *Uromyces*.

This genus occupies an intermediate position between *Uromyces* and the less advanced genera, *Phragmidium*, etc., as is shown by the fact that many species tend to form one-celled teleutospores (mesospores) indistinguishable from those of *Uromyces*, while others have spores with three or more cells, arranged as in *Phragmidium*, *Triphragmium*, *Sphaerophragmium*, etc.

The number of species is enormous, more than 1300 are already known. The genus must therefore be subdivided, but no quite satisfactory classification has as yet been discovered. Schröter's and Fischer's separate nearly allied species, while Arthur's is a pathless chaos. As a temporary measure, instead of adding a new imperfect scheme to those already existing, the species are here arranged on the plan adopted in Sydow's Monographia, in the order of the families and genera on which they are parasitic; this has the advantage that it does, to a great extent, bring nearly allied species close together, while it is at the same time very convenient for consultation. In each family the genera are arranged in the order familiar to British botanists, but the families themselves are in the order usually adopted on the continent, because that will before long be accepted here also.

1. *Puccinia Tripolii* Wallr.

Puccinia Tripolii Wallr. Fl. Crypt. Germ. ii. 223. Cooke, Micr. Fung. p. 207; Grevillea, iii. 180.

P. Asteris Duby, Bot. Gall. ii. 888. Plowr. Grevillea, ii. 48; Ured. p. 215. Sacc. Syll. vii. 687 p.p. Sydow, Monogr. i. 15 p.p.

Teleutospores. Sori amphigenous, confluent into rather large, pulvinate masses, hard, compact, very dark-brown: spores oblong-clavate or clavate, rounded above or somewhat narrowed and much thickened (as much as 8μ), slightly constricted, generally attenuated downwards, smooth.

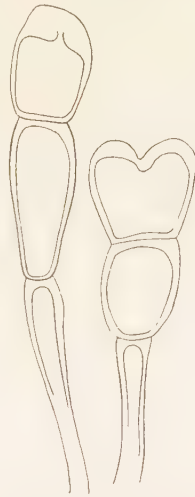


Fig. 80. *P. Tripolii*. Teleutospores (one abnormal).

pale clear-brown, $45-60 \times 20-25 \mu$; pedicels brownish, persistent, thick, about as long as the spore or longer; no mesospores were seen, but some irregular spores.

On *Aster Tripolium*. New Pittsboro, 1870 (Herb. Berk.); Wolferton Beach, King's Lynn, July—November, 1873 (Plowright). (Fig. 80.)

The greyish tinge mentioned by Plowright seems to be due to germ-tubes issuing from the spores of this *Leptopuccinia*. This species is decidedly different from the American forms with which it is united by Sydow; there are no spots, the colour of the spore is paler, the apex not so much thickened, and the sori are not confined to the lower leaf-surface. Many spores were observed bitid at the summit, but not owing to germination, which had not taken place in them.

DISTRIBUTION: Northern and Central Europe, Siberia.

2. *Puccinia Virgaureæ* Lib.

Xyloma Virgaureæ DC. Flor. fr. vi. 158.

Puccinia Virgaureæ Lib. Crypt. Arduen. iv. No. 393. Cooke, Handb. p. 500; Micr. Fung. p. 206. Plowr. Ured. p. 203. Sacc. Syll. vii. 679. Sydow, Monogr. i. 151. Fischer, Ured. Schweiz, p. 363, f. 264.



Fig. 81. *P. Virgaureæ*.
Teleutospores.

Teleutospores. Sori hypophyllous, minute, crowded in stellate or dendritic clusters, on round, yellowish, purple-centred spots, compact, shining, black; spores oblong, clavate or fusoid, above rounded, attenuated or truncate, very much thickened (as much as 12μ) and darker or with a paler hood-like cap, hardly constricted, tapering below, smooth, yellow-brown, paler downwards, $30-56 \times 12-20 \mu$; pedicels somewhat hyaline, half as long as the spore.

On *Solidago Virgaurea*. August and September. Uncommon; Surrey, etc. (Fig. 81.)

The sori are arranged in a radiating fashion; they are surrounded each by a thick fence of dark-brown paraphyses, remain long covered by

the epidermis and resemble rather a *Dothidea* or *Asteroma* than a *Puccinia*. The spores bear a slight resemblance to those of *P. Poarum*, but are more fusiform, and much more thickened at the apex. Mixed with them are sometimes a number of mesospores.

DISTRIBUTION: Europe, except the southern parts.

3. *Puccinia Millefolii* Fekl.

Puccinia Millefolii Fekl. Symb. Myc. p. 55. Cooke, Micr. Fung. p. 207.

Plowr. Ured. p. 215. Sydow, Monogr. i. 2. Fischer, Ured.

Schweiz, p. 296, f. 216.

Teleutospores. Sori amphigenous, on indistinct spots, minute, roundish or irregular, generally scattered, compact, dark-brown; spores oblong or clavate, rounded or gently attenuated at the apex and thickened ($4-9\mu$), constricted, more or less tapering below, smooth, pale-brownish, $35-50 \times 13-19\mu$; pedicels yellowish above, thick, persistent, about 40μ long; a few mesospores are sometimes intermixed.

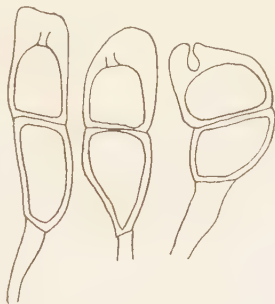


Fig. 82. *P. Millefolii*. Teleutospores.

On *Achillea Millefolium*. For-
den; St Leonards. August—October. (Fig. 82.)

Plowright demonstrated (*l.c.* p. 216) that this species is quite distinct from *P. Tripolii*, with which it had been previously united, and his conclusion has been confirmed by Magnus and others. The species is rather uncommon; there is a closely allied one on *A. Ptarmica* (*P. Ptarmicæ* Karst.) which has not yet been seen in Britain. The spores of *P. Millefolii* germinate as soon as mature.

DISTRIBUTION: Central and Western Europe.

4. *Puccinia Chrysanthemi* Roze.

Uredo Chrysanthemi Roze; Plowright in Trans. Brit. Myc. Soc. i. 98.

Puccinia Chrysanthemi Roze, Bull. Soc. Myc. Fr. 1900, p. 92. Sacc.

Syll. xvi. 296. Sydow, Monogr. i. 46, 854. McAlpine, Rusts of
Australia, p. 153, f. 251—5, and pl. E, f. 21. Fischer, Ured.

Schweiz, p. 190, f. 150.

P. Chrysanthemi-chinensis Henn. in Hedwig. xl. 26 (1901).

Uredospores. Sori generally hypophyllous, on irregular pallid-yellow or brownish spots, scattered or in clusters, about 1—1½ mm. diam. often circinate, pulverulent, snuff-brown; spores globose to ellipsoid, delicately echinulate, brown, 24—52 × 17—27 μ , mostly with three germ-pores.



Fig. 83. *P. Chrysanthemi*. Uredospore (British).

[*Teleutospores.* Mixed with the uredospores, oblong or ellipsoid, rounded and slightly thickened above, usually rounded or somewhat tapering at base, scarcely constricted, delicately verruculose, chestnut-brown, 35—57 × 20—25 μ ; pedicels thick, hyaline, persistent, 35—60 μ long; mesospores subglobose or pyriform, slightly thickened at the summit, 32—37 × 20—21 μ .]

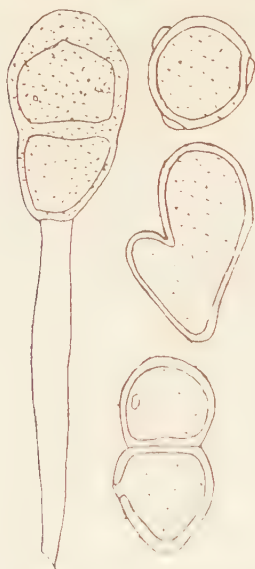


Fig. 84. *P. Chrysanthemi*. Teleutospores and uredospores, one abnormal (after Fischer).

• On leaves of *Chrysanthemum indicum* and *C. sinense* (not on other species of the genus, much less on other genera of Compositæ), in greenhouses, all the year round. The leaves that are attacked soon flag and die. (Figs. 83, 84.)

This species is said to be very common in Japan. It was first observed in England in 1895, and has been found in other European countries and in North America; in 1904 it reached Australia and New Zealand.

In Japan it produces teleutospores in separate sori, which are hypophyllous, roundish, dark-brown and naked, but in Europe the teleutospores have been rarely seen, though mesospores occasionally occur. Abnormal and 2-celled uredospores (as well as 3- or 4-celled teleutospores) have been described and figured by Roze, Jacky and Fischer; but these I have not seen in British specimens.

Since, under the conditions in which the plants are grown here, the young shoots appear above ground before the old ones die away, it is probable that the parasite maintains itself by the uredospores alone; the alternative would be the possession of a perennial mycelium, which has not

been found (Gibson, 1904, p. 188). If that is so, the disease can easily be kept in check by rigid cleanliness and by spraying at intervals with very dilute Bordeaux mixture or, better still, potassium sulphide solution. Remove and burn all attacked leaves as soon as seen, water carefully without wetting the leaves, choose resistant varieties (*e.g.* "October Sun" and "William Tricker" are said to be immune), and there will be little fear of an epidemic of the disease.

DISTRIBUTION: Europe, Japan, North America, Australia.

5. *Puccinia Leucanthemi* Pass.

Puccinia Leucanthemi Pass. in Hedw. 1874, p. 47. Sacc. Syll. vii. 705. Sydow, Monogr. i. 116, f. 95.

P. Asteris var. *Chrysanthemi-Leucanthemi* Massal. in Bull. Soc. Bot. Ital. 1900, p. 258. Sacc. Syll. xvi. 297. Trans. Brit. Myc. Soc. iii. 224.

Teleutospores. Sori amphigenous, generally hypophyllous, often also on the petioles, scattered or often circinate on indistinct spots, or confluent into compact cushions 2—5 mm. wide, reddish-brown; spores oblong or subclavate, somewhat rounded or more often narrowed at the apex, much thickened above (up to 14μ), constricted, tapering downwards, smooth, yellowish, $40\text{--}70 \times 14\text{--}24\mu$; pedicels hyaline, thick, about as long as the spore.

On *Chrysanthemum Leucanthemum*. Very rare. Lamorna Cove, Cornwall, September, 1906 (F. J. Chittenden). (Fig. 85.)



Fig. 85. *P. Leucanthemi*. Teleutospores, from an original specimen issued by Passerini.

Only recorded for Britain and Italy. The similarity of the spores to the teleutospores of *Puccinia Æcidii-Leucanthemi* Fisch., which has its æcidiospores on *C. Leucanthemum* and its teleutospores on *Carex montana*, seems to indicate that this is one of those instances, like *P. fusca* and *P. Pruni-spinosae*, which give us a glimpse into the mode of evolution of the Uredinales.

6. **Puccinia Absinthii** DC.

Trichobasis Artemisiae Berk. ; Cooke, Micr. Fung. p. 223.

Puccinia Discoidearum Link ; Cooke, Micr. Fung. p. 206.

P. Tanacetii Plowr. Ured. p. 189 p.p. Sacc. Syll. vii. 637 p.p.

P. Absinthii DC. Flor. fr. vi. 56. Sydow, Monogr. i. 11. Fischer, Ured. Schweiz, p. 188, f. 148.

Uredospores. Sori generally hypophyllous, on yellowish-brown or indeterminate spots, scattered or aggregated, not confluent, minute, roundish, pulverulent, pale-brown: spores globose to ovoid, echinulate, pale yellowish-brown, $20-35 \times 15-26 \mu$, mostly with three subequatorial germ-pores.

Teleutospores. Sori amphigenous, but generally on the lower surface or sometimes on the stems, similar to the uredo-sori but occasionally confluent, soon naked, dark-brown or blackish; spores oblong to oblong-clavate, rounded and thickened ($3-7 \mu$) above, constricted, slightly attenuated below, the upper cell punctate or verruculose, the lower frequently smooth, especially at the base, brown, $38-62 \times 20-27 \mu$; pedicels hyaline, thick, persistent, as much as 80μ long.

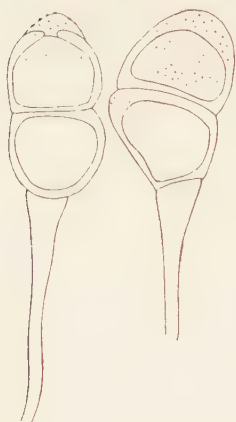


Fig. 86. *P. Absinthii*. Teleutospores, on *A. Absinthium*.

On *Artemisia Absinthium*, *A. maritima*, *A. vulgaris*. July—September. Rather uncommon. Also recorded in Switzerland on *A. campestris*. (Fig. 86.)

The germ-pores of both kinds of spores are covered with paler, swollen caps. *P. Tanacetii*, which was formerly united with this species, possesses on the average narrower and shorter teleutospores, though in each these spores are said to be marked in a similar way, chiefly in the upper half. But the markings of *P. Absinthii* are stronger and less likely to escape observation, especially on the pore-caps of both cells.

DISTRIBUTION : Europe, Siberia, Japan, North America

7. **Puccinia Tanaceti** DC.

Puccinia Tanaceti DC. Flor. fr. ii. 222. Cooke, Micr. Fung. p. 207.

Plowr. Ured. p. 189 p.p. Sacc. Syll. vii. 657. Sydow, Monogr. i.

161. Fischer, Ured. Schweiz, p. 185, f. 146.

P. Discoidearum Link; Cooke, Handb. p. 499 p.p.

Uredospores. Sori amphigenous, scattered, minute, not confluent, orbicular, pallid-brown; spores subglobose or broadly ellipsoid, echinulate, yellow-brown, $25-32 \times 16-25 \mu$, with three germ-pores, each covered by a convex colourless cap.

Teleutospores. Sori mostly hypophyllous, similar, but more compact and blackish, $\frac{1}{2}-\frac{3}{4}$ mm. diam.; spores ellipsoid or

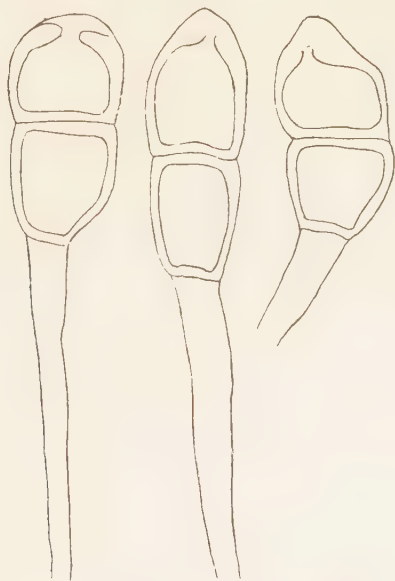


Fig. 87. *P. Tanaceti*. Teleutospores.

oblong, more or less rounded at both ends, thickened above (up to 7μ), delicately verruculose(?) especially in the upper part, rich-brown, $32-44 \times 16-24 \mu$; pedicels hyaline, thick, persistent, as much as 120μ long.

On *Tanacetum vulgare*. Not common. August, September. (Fig. 87.)

Formerly united with *Puccinia Absinthii*, from which it is distinguished by its (on the average) narrower and shorter teleutospores, with longer pedicels. I could not see in any case that the teleutospores were verruculose, as they are said to be.

DISTRIBUTION: North-western and Central Europe.

8. *Puccinia expansa* Link.

Puccinia expansa Link, Sp. Pl. vi. 2, p. 75. Sydow, Monogr. i. 146.

Fischer, Ured. Schweiz, p. 182, f. 141—2.

P. Senecionis Cooke, Micr. Fung. p. 207. Plowr. Ured. p. 209, (non Lib.).

Teleutospores. Sori amphigenous, but generally hypophyllous.

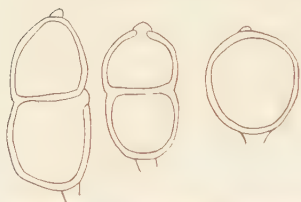


Fig. 88. *P. expansa*. Teleutospores and mesospore, on *S. Jacobaea*.

on round yellowish or brownish spots, densely crowded and confluent in roundish clusters 5—8 mm. broad, blackish-brown; spores ovate or broadly ellipsoid, rounded at both ends, with a minute paler apical papilla, hardly constricted, smooth, brown, $30-40 \times 19-30 \mu$, but sometimes smaller; pedicels

hyaline, very short; an occasional mesospore is seen.

On *Senecio aquaticus*, *S. Jacobaea*. Not common. July—September. (Fig. 88.)

The sori of this species are chiefly on the underside of the leaf; they are collected into roundish or elongated groups and open by a small round pore, after the manner of some aecidia, so that, when the spores have fallen out, the group looks like a honeycomb. *P. glomerata* is said to be distinguished by its paler, narrower and longer spores with a smaller papilla, and by having the sori on both leaf-surfaces. I think the two species are the same so far as our specimens are concerned, but have followed Sydow's Monographia *pro tem*. Plowright has confused the characters of the two, partly because he thought his species on *S. aquaticus* was *P. Senecionis* Lib., which is incorrect. The true *P. Senecionis* Lib. has not been found in Britain.

DISTRIBUTION: Central Europe, Holland, California.

9. *Puccinia glomerata* Grev.

Puccinia glomerata Grev. in Berk. Eng. Fl. v. 365. Cooke, Handb. p. 500; Micr. Fung. p. 206. Plowr. Ured. p. 209. Sydow, Monogr. i. 148, t. 8, f. 125.

Teleutospores. Sori amphigenous, on brown orbicular spots, densely gregarious and confluent in roundish clusters, 3—6 mm. broad, occupying the whole spot, often circinate, long covered by the epidermis, at length rather pulverulent, deep-brown; spores ovate to oblong, with a very minute paler apical papilla, hardly constricted, rounded or slightly attenuated below, smooth, pale-brown, $30-45 \times 16-24 \mu$; pedicels hyaline, very short.

On *Senecio Jacobaea*. August—November. Not common.

Closely allied to the preceding species, but said to be distinguished by its paler, narrower and longer spores which are provided with a smaller apical papilla. Moreover, the sori are said to be less dark in colour (not *darker* as Plowright states), and are distributed more uniformly on both leaf-surfaces. Nevertheless, I suspect they are identical.

DISTRIBUTION: Belgium.

10. *Puccinia Carlinæ* Jacky.

Puccinia Hieracii Mart.; Plowr. Ured. p. 184 p.p.

P. Carlinæ Jacky, Compos.-Pucc. p. 59, f. 14. Sacc. Syll. xvi. 297.

Sydow, Monogr. i. 35. Fischer, Ured. Schweiz, p. 216, f. 167.

Spermogones. Epiphyllous and on the petioles, singly or in groups.

Uredospores. Sori amphigenous, without evident spots, scattered, not confluent, minute, punctiform, pulverulent, brown; spores globose or broadly ellipsoid, very delicately echinulate, pallid-brown, $24-30 \times 20-25 \mu$; epispore uniformly thick, with three germ-pores.

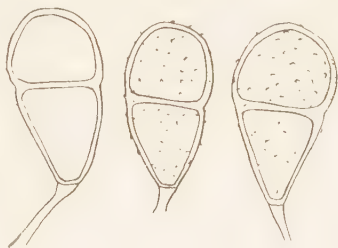


Fig. 89. *P. Carlinæ*. Teleutospores.

Teleutospores. Sori similar, but blackish-brown; spores ellipsoid to obovate-oblong, rounded at both ends or more often attenuated downwards, not thickened above, hardly constricted, delicately verruculose, brown, $25-35 \times 16-20 \mu$; pedicels hyaline, short.

On *Carlina vulgaris*. July—October. Not common. (Fig. 89.)

Distinguished from *P. Cirsii*, which it much resembles, by the larger uredospores, with very delicate hardly perceptible spines, and by the slightly smaller teleutospores which are more frequently narrowed below. But no cultures seem to have been made to prove their distinctness.

DISTRIBUTION: Central and Northern Europe.

11. *Puccinia Bardanae* Corda.

Puccinia Hieracii Plowr. Ured. p. 184 p.p.

P. Bardanae Corda, Icones, iv. 17. Sydow, Monogr. i. 113. Fischer, Ured. Schweiz, p. 221, f. 173.

Spermogones. Similar to those of *P. Cirsii*.

Uredospores. Sori of two kinds; *primary* epiphyllous, on discoloured rounded or irregular spots, in concentric rings round the spermogones, sometimes confluent, 1—5 mm. broad, flat, surrounded by the cleft epidermis, pulverulent, cinnamon; *secondary* amphigenous, without spots, about $\frac{1}{2}$ —1 mm. diam., scattered or gregarious; spores globose to ellipsoid, echinulate, pale-brown, $26\text{--}30 \times 22\text{--}27\ \mu$, with three (rarely four) germ-

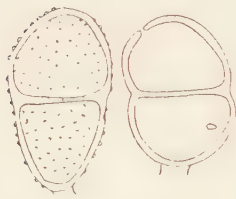


Fig. 90. *P. Bardanae*. Teleutospores, on *A. Lappa* (Austria).

pores.

Teleutospores. Sori amphigenous, generally hypophyllous, without spots, scattered or in places densely gregarious, $\frac{1}{2}$ —1 mm. diam., rounded, pulverulent, black-brown; spores ellipsoid, rounded at both ends, not thickened, gently constricted, delicately verruculose, dark-brown, $30\text{--}42 \times 22\text{--}27\ \mu$; pedicels hyaline, short.

On *Arctium Lappa*. September, October. A doubtful native; I have seen no British specimens. Description after Sydow. (Fig. 90.)

Distinguished from *P. Cirsii* by its larger teleutospores and by its two kinds of uredo-sori. Jacky demonstrated the distinctness of the two species by experimental cultures (Centralbl. f. Bakt. 2. ix. 796); also that *P. Bardanae* could not be transferred to *Taraxacum*.

DISTRIBUTION: Europe only.

12. *Puccinia tinctoriæ* Magn.

Puccinia Compositarum var. *Serratulae* Cooke, Exsicc. no. 33.

P. tinctoriæ Magn. in Abhand. Nat. Gesell. Nürnberg, 1900, xiii. 37 ;
Ber. deutsch. Bot. Gesell. 1893, pl. 21, f. 27—8. Sydow, Monogr.
i. 150, f. 127.

Uredospores. Sori amphigenous, on inconspicuous pallid spots, scattered, minute, roundish, pulverulent, dark-cinnamon ; spores globose to ellipsoid, echinulate, brown, $24-40 \times 19-26 \mu$; epispore with two germ-pores towards the summit.

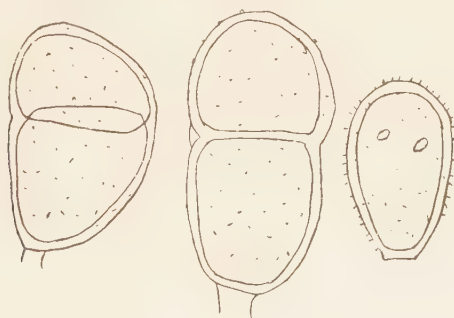


Fig. 91. *P. tinctoriæ*. Teleutospores and uredospore (from Cooke's specimens).

Teleutospores. Sori similar, but blackish ; spores ellipsoid to oblong, rounded at both ends, not thickened above, hardly constricted, delicately verruculose, brown, $27-60 \times 19-30 \mu$; pedicels hyaline, up to 14μ long ; epispore thin.

On leaves of *Serratula tinctoria*. Apparently very uncommon ; Belton Wood, Highgate (M. C. Cooke). Teleutospores, July—September. (Fig. 91.)

DISTRIBUTION : France, Sweden, Germany, Austria, Italy, Siberia.

13. *Puccinia Centaureæ* DC.

Puccinia Compositarum Sch. ; Cooke, Handb. p. 499 ; Micr. Fung. p. 206 p.p.

P. Centaureæ DC. Flor. fr. vi. 595. Cooke, Micr. Fung. p. 207.
Plowr. Ured. p. 186. Sydow, Monogr. i. 39. Fischer, Ured. Schweiz, p. 222, f. 174—5.

Spermogones. Chiefly epiphyllous, in little clusters, orange.

Uredospores. Sori generally hypophyllous, on yellowish or brownish spots (spots sometimes none), *primary* rather large,

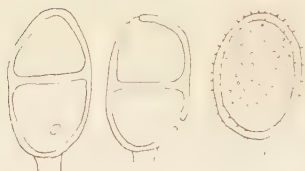


Fig. 92. *P. Centaureae*. Teleutospores and uredospore.

secondary very minute, much scattered, pulverulent, brown; spores globose to ellipsoid, aculeolate, brown, $22-30 \times 16-28 \mu$, with three (or two) germ-pores.

Teleutospores. Sori similar, but blackish-brown; spores ellipsoid or somewhat obovate, rounded at both ends, not thickened above, not or hardly constricted, delicately verruculose, chestnut-brown, $24-40 \times 16-25 \mu$; epispore thin; pedicels hyaline, thin, generally very short.

On *Centaurea nigra*. Teleutospores, August—November. Common. (Fig. 92.)

As Plowright says, there are two generations of uredospores. The primary uredospores, which are the equivalent of the æcidiospores, accompanied by spermogones, appear in May, and are followed by the secondary uredospores, which form much smaller sori. The former, however, do not occur on every infested plant, being only produced from direct infection by the basidiospores. The primary uredospores are widely scattered by the wind; Plowright proved that they produce the secondary spores in about fourteen days. Fischer and Jacky record this also on *C. Scabiosa*, but the Pucciniae on other species of *Centaurea* are considered to be distinct species or else biological races.

DISTRIBUTION: Europe, Asia Minor, Siberia, North America.

14. *Puccinia Cyani* Pass.

Uredo Cyani Schleich. Plant. Helv. 95.

Puccinia suaveolens var. *Cyani* Winter, Pilze Deutschl. p. 190. Plowr.

Ured. p. 183. Sacc. Syll. vii. 633.

P. Cyani Pass. in Rab. Fung. Eur. 1767. Sydow, Monogr. i. 38.

Spermogones. A few mixed with the primary uredo-sori.

Uredospores. Sori generally hypophyllous, without spots, scattered or crowded, minute, roundish, pulverulent, cinnamon;

spores globose to ellipsoid, delicately echinulate, yellow-brown, $22-30 \times 19-24 \mu$, with two germ-pores.

Teleutospores. Sori amphigenous and on the stems, scattered, minute, punctiform, pulverulent, blackish-brown; spores broadly ellipsoid, rounded at both ends, not thickened above, not constricted, very delicately verruculose, chestnut-brown, $30-35 \times 22-27 \mu$, sometimes longer; pedicels hyaline, short.

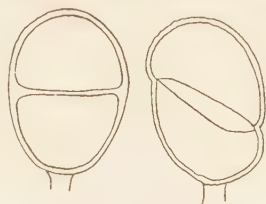


Fig. 93. *P. Cyani*.
Teleutospores.

On *Centaurea Cyanus*. Not uncommon in gardens. June—September. (Fig. 93.)

There is a similar species, *P. montana*, which occurs on the continent on *Centaurea montana*; it is distinguished by the much coarser warts of the teleutospores, which are also relatively longer. Both these species, like *P. obtegens*, permeate the whole plant with the mycelium of the primary uredospores, but such infested plants of *Centaurea* can flower freely, while those of *Cirsium arvense* never do. The mycelium of the secondary uredospores, mixed with teleutospores, is more strictly localised.

DISTRIBUTION: Western and Central Europe.

15. *Puccinia Carduorum* Jacky.

Puccinia Hieracii Plowr. Ured. p. 185 p.p., see also p. 216.

P. Carduorum Jacky, Composit.-Puccin. p. 58. Sacc. Syll. xvi. 297.
Sydow, Monogr. i. 33.

Uredospores. Sori generally hypophyllous, on very indistinct spots, scattered, minute, pulverulent, cinnamon; spores globose or subglobose, densely echinulate, pale-brown, $22-28 \mu$, with three germ-pores.

Teleutospores. Sori similar, but dark-brown; spores variable, oblong to ovate, rounded above, not thickened, hardly at all constricted, rounded below, verruculose, brown, $25-38 \times 17-24 \mu$; epispore thin; pedicels hyaline, short.

On *Carduus crispus*, *C. nutans*. Not common; Yorkshire, Clare Island, etc.

This species was formerly undistinguished from the numerous forms on allied species of Compositae, until Lacky proved experimentally in 1899) that it is confined to the sub-genus *Carduus*, and could not be transferred to *Oniscus* or *Cirsium*. The uredo form described above (after Sydow) is the secondary uredo; the primary form, which does not always occur, is described as amphigenous and larger, often on the mid-ribs 2—4 mm. long, and remaining long covered by the epidermis.

DISTRIBUTION: Europe and Siberia.

16. *Puccinia Cardui-pycnocephali* Syd.

Puccinia Cardui-pycnocephali Sydow, Monogr. i. 34, f. 35. Masee, Journ. Bot. xvi. 152; Trans. Brit. Myc. Soc. (1909), iii. 123.

Uredospores. Sori hypophyllous, without spots, scattered, minute, pale-brown; spores globose or subglobose, very delicately echinulate, pale-brown, 22—26 μ .

Teleutospores. Sori similar, hidden in the tomentum of the host, brown; spores oblong, rounded above and more or less so below, not thickened, hardly constricted, smooth, pale-brown, 38—50 $\times$ 16—23 μ ; epispore thin; pedicels thin, hyaline, up to 40 μ long, but deciduous.

On leaves and stems of *Carduus pycnocephalus*. Very rare: Sidmouth (Dr Mayor), and between Eastbourne and Hastings (G. Masee). Only recorded for Britain and Italy. July, August.

Distinguished from *P. Carduorum* by its longer teleutospores, which are smooth, and not plainly verruculose as in that species. But sometimes the spores are said to approach those of *P. galatica* Sydow, which occurs on the same host in Asia Minor, in being smaller, darker-coloured, thick-walled, and delicately punctate. According to Masee (*l.c.*) these are rather two poles of one species than two distinct species.

17. *Puccinia Cirsii* Lasch.

Trichobasis Cirsii Lasch; Cooke, Micr. Fung. p. 224.

Puccinia Cirsii Lasch, in Rab. Fung. Eur., no. 89. Cooke, Grevillea, iv. 109; Micr. Fung. p. 206. Sydow, Monogr. i. 55. Fischer, Ured. Schweiz, p. 217, f. 168—171.

Uredospores. Sori epiphyllous or hypophyllous, on paler spots, scattered, minute, girt by the epidermis, pulverulent, cinnamon; spores globose to ovate, echinulate, pale chestnut-brown,

22—28 × 19—24 μ , with three more or less equatorial germ-pores each provided with a thickening.

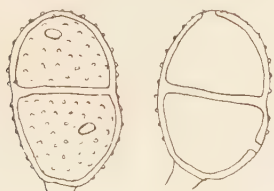


Fig. 94. *P. Cirsii*. Teleutospores, on *C. palustre*, from Hereford.

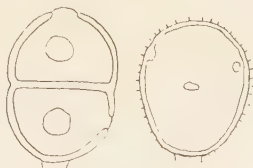


Fig. 95. *P. Cirsii*. Teleutospore and uredospore, on *C. lanceolatum*.

Teleutospores. Sori mostly hypophyllous only, similar, but blackish-brown or black: spores ellipsoid or somewhat obovate, rounded at both ends, not thickened above, hardly constricted, verruculose or merely punctate, chestnut-brown, 25—38 × 17—25 μ ; epispore thin; pedicels hyaline, very short.

On *Cirsium*, Dupplin Castle, Perth (M. C. Cooke). On *C. pratense*, Ballyquirke Lake, Co. Galway (communicated by J. Adams); Earlswood Lakes, near Birmingham. On *C. palustre*, Hereford, Seckley Wood, Barnt Green, etc. Uredospores from March; teleutospores, June—November. (Figs. 94, 95.)

There is no mention of this in Plowright's Uredineæ, or in the Trans. Brit. Myc. Soc. (Plowright's list), but it is probably not uncommon. It occurs frequently on the radical leaves, and can be easily distinguished from *P. Cnici-oleracei* by the presence of the uredospores and the non-circinate teleuto-sori, as well as by the absence of the apical thickening. Fischer records it from Switzerland on many species of *Cirsium* (but not on those mentioned here), and also assigns to it spermatogones on the upper leaf-surface and petiole; I have not been able to find any trace of these in our British specimens. The uredospores, seen in water, sometimes appear quite smooth, as Cooke describes them. The teleutospores have the upper pore at the summit or at the side, the lower pore just beneath the septum or lower down; they are at times faintly granulated, at others distinctly verruculose. Mesospores are rare.

I have also a number of specimens on *C. lanceolatum* from Droitwich, Wyre Forest, etc., bearing a great similarity to *P. Cirsii-lanceolati* Schröt., but the differences from *P. Cirsii* are so slight and elusive that, as the æcidial stage by which the former is distinguished has not yet been found in Britain, it is better for the present to place them under *P. Cirsii*.

DISTRIBUTION: Europe, Siberia, Japan, North America.

18. **Puccinia Cnici-oleracei** Pers.

Puccinia Cnici-oleracei Pers. in Desm. Cat. des Pl. omis., p. 24.

Sydow, Monogr. i. 58, pl. 3, f. 47. Fischer, Ured. Schweiz, p. 292, 594, f. 213.

P. Cardui Plowr. Ured. p. 216.

Teleutospores. Sori hypophyllous, on discoloured roundish spots, minute, circinate, but mostly confluent in large patches as much as 5 mm. diam. which remain for a long time covered by the epidermis, compact, blackish-brown: spores clavate or subfusiform, rounded or rarely somewhat conical above, very

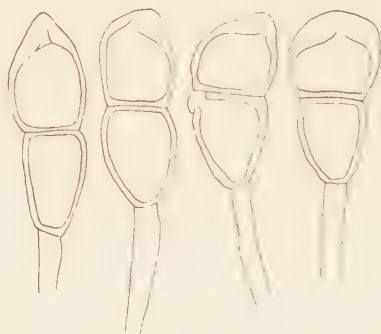


Fig. 96. *P. Cnici-oleracei*. Teleutospores, on *C. lanceolatum*.

much thickened ($5-10\ \mu$), constricted, attenuated below, smooth, yellowish-brown, $38-56 \times 14-21\ \mu$; pedicels yellowish-hyaline, thick, persistent, as much as $50\ \mu$ long.

On *Cirsium lanceolatum*, *Carduus crispus* (?). August—October. Not uncommon on the former. (Fig. 96.)

This is one of the species in which the upper cell separates from the lower one. It is doubtful if *Puccinia Syngenesiarum* (Cooke, Handbook, p. 499; Mier. Fung. p. 206) belongs entirely here, as the figure in the latter work (pl. 4, f. 64) does not give the true form of the teleutospore; but the majority of the specimens issued by him under that name are this species. It is very questionable if this species occurs on *Carduus crispus*, on which it is recorded by Plowright.

DISTRIBUTION: in a few places in Europe.

19. **Puccinia obtegens** Tul.

Caeoma obtegens Link, Obs. ii. 27.

Trichobasis suaveolens Lév.; Cooke, Handb. p. 530; Micr. Fung. p. 226, pl. vii. figs. 151—3.

Puccinia obtegens Tul. Ann. Sci. Nat. ser. 4, ii. 87 (1854). Sydow, Monogr. i. 53.

P. suaveolens Rost. Bot. Zeit. 1874, p. 556. Plowr. Ured. p. 182 p.p. Sacc. Syll. vii. 633 p.p. Fischer, Ured. Schweiz, p. 219, f. 172.

Spermogones. Chiefly hypophyllous, a few epiphyllous, crowded, covering the whole surface of the leaf, of a bright honey-yellow colour and a pleasant smell.

Uredospores. *Primary* sori hypophyllous, occupying the whole surface of the leaf, minute, crowded, often confluent, pulverulent, reddish-brown, then darker; *secondary*, more scattered; spores globose to broadly ellipsoid, echinulate, pale-brown, $21\text{--}28\ \mu$, with three irregularly placed germ-pores.

Teleutospores. Sori similar, always dark-brown; spores ovate to ellipsoid, rounded at both ends, or somewhat tapering below, not thickened above but with a low flat pore-cap, hardly constricted, delicately verruculose, brown, $26\text{--}42 \times 17\text{--}25\ \mu$; epispore thin; pedicels hyaline, thin, short.

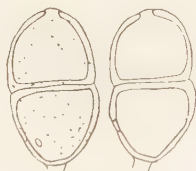


Fig. 97. *P. obtegens*.
Teleutospores.

On *Cirsium arvense* (*Carduus arvensis*).
Very common. (Fig. 97.)

The life-history of this species is peculiar. In spring the mycelium permeates the host in every part. The affected plants can be recognised immediately by their pale-green colour and spindly appearance; they never flower. The spermogones are first seen towards the end of April, and are easily detected by their bright colour, and their strong perfume, resembling that of privet-flowers; the uredospores follow on the same leaves during May. From these primary uredospores, a second generation arises on other plants about July, and forms secondary uredospores and teleutospores in sori which are more scattered, never confluent, and darker brown. This generation is not accompanied by spermogones. The mycelium of these sori is localised to the infected spots and the host does not suffer so severely. The sori of the primary uredospores rarely bear a few teleutospores intermixed, but the secondary sori abound with them from September to November, and it is from the germination of

these latter that new infections arise in the spring as soon as the shoots appear. The hibernation of the mycelium in the rhizome, which is stated by Plowright, has not been proved.

The germ-pores are very easy to see in the uredospores of this species and its allies. Each is often surrounded by a border like a bordered pit, an appearance caused by a thickening of the membrane around and over the pit. As usual the appearance of the spore changes according as it is wet or dry; if wet, it may appear merely punctate; if dry, it is seen to be densely and coarsely echinulate.

DISTRIBUTION: Northern and Central Europe, Siberia, North America.

20. *Puccinia Andersoni* B. et Br.

Puccinia Andersoni B. et Br. Ann. Nat. Hist. ser. 4, xv. 35. Cooke, Micr. Fung. p. 206; Grevillea, iii. 179. Plowr. Ured. p. 204. Sacc. Syll. vii. 710. Sydow, Monogr. i. 58.

Teleutospores. Sori hypophyllous, seated on round yellow spots 1—1½ cm. diam. with a brown border, almost concealed by the pubescence of the leaf, minute, but densely crowded in flat circular clusters which are few on each leaf, compact, blackish-brown or purplish-black; spores oblong to clavate, rounded or conically thickened (8—10 μ) above, slightly constricted, smooth, pale-brown, 40—54 $\times$ 16—22 μ ; pedicels brownish, stout, persistent, as long as the spore or longer; a number of mesospores are found intermixed.

Fig. 98. *P. Andersoni*. Teleutospores and mesospore.

On *Cirsium heterophyllum*. June—October. A striking and rare species. Glen Ogle (Rev. M. Anderson), Den of Airlie (Mr Gardiner), Ingleton and Grassington, Yorkshire (H. T. Soppitt), Alston, Cumberland (J. G. Baker). (Fig. 98.)

DISTRIBUTION: in a few places in Europe.

21. **Puccinia Lapsanæ** Fekl.

Æcidium Lapsanæ Schultz, Prod. Flor. Starg. p. 454. Cooke, Journ.

Bot. ii. 38, pl. 14, f. 2; Handb. p. 543; Micr. Fung. p. 198.

Trichobasis Lapsanæ Cooke, Micr. Fung. p. 224.

Puccinia Lapsanæ Fekl. Symb. Myc. p. 53. Cooke, Micr. Fung.

p. 207. Plowr. Ured. p. 149. Sacc. Syll. vii. 607. Sydow,

Monogr. i. 112. Fischer, Ured. Schweiz, p. 203, f. 159.

Spermogones. Crowded in little clusters, epiphyllous, honey-coloured.

Æcidiospores. *Æcidia* amphigenous, somewhat crowded on large, roundish, purple spots, flattish, with torn white reflexed margin; spores subglobose or ovate, nearly smooth, orange, $16-21 \times 13-17 \mu$.

Uredospores. Sori amphigenous, very minute, round, very numerous, often confluent, pulverulent, chestnut-brown: spores globose to ovate, delicately echinulate, pale-brown, $17-22 \times 15-18 \mu$, with two germ-pores.



Fig. 99. *P. Lapsanæ*.
Teleutospore.

Teleutospores. Sori amphigenous, minute, scattered, numerous, pulverulent, blackish-brown; spores ellipsoid or ovate, rounded at both ends, not thickened above, scarcely constricted, very delicately punctate, chestnut-brown, $22-33 \times 17-26 \mu$; pedicels hyaline, slender, short, often oblique.

On leaves and stems of *Lapsana communis*. Very common. *Æcidia*, March—May; uredospores, April—June; teleutospores, June—September. (Fig. 99.)

The *æcidium* of this species shares with those on *Ranunculus Ficaria* and *Potentilla Fragariastrum* the distinction of being the earliest Uredine to make its appearance in the spring. It may be found on the young leaves of the seedlings almost as soon as they are formed. Plowright demonstrated (Expt. 499, May, 1885) that all three spore-forms belong to the same life-cycle. The mycelium of the *æcidia*, when occurring on the petioles, causes them to become pale and swollen; on the leaves it often produces conspicuous purple spots which bear the spermogones on the upper surface.

DISTRIBUTION: Europe, Syria, Japan.

22. **Puccinia Cichorii** Bell.

Uredo Cichorii DC. Flor. fr. vi. 74.

Puccinia Hieracii Mart. ; Plowr. Ured. p. 184 p.p.

P. Cichorii Bell. in Kickx, Fl. Fland. ii. 65. Sydow, Monogr. i. 49.

Fischer, Ured. Schweiz, p. 227, f. 179. McAlpine, Rusts of Australia, p. 154, f. 61 and pl. D, f. 18.

Uredospores. Sori amphigenous or on the stems, numerous, scattered, sometimes confluent, minute, pulverulent, surrounded by the torn epidermis, cinnamon; spores globose to ellipsoid, echinulate, yellowish-brown, $21-27\ \mu$; epispore moderately thick, with two germ-pores.

Teleutospores. Sori similar, but blackish-brown; spores ellipsoid, rarely obovate, rounded above and not thickened, hardly constricted, generally rounded below, smooth or faintly verruculose, brown, $27-38 \times 19-25\ \mu$; epispore thin; pedicels hyaline, short, deciduous.

On *Cichorium Intybus*. Rare. August—October.

This species closely resembles *Puccinia Hieracii*, and there seem to have been no cultures which give any information about its distinctness. It is therefore separated merely on the ground of the difference of the genus of the host; see under *P. Hieracii*.

DISTRIBUTION: Europe; introduced into Australia.

23. **Puccinia Hypochæridis** Oud.

Puccinia Hypochaeridis Oud. in Nederl. Kruidk. Archief. ser. 2, i. 175.

Sydow, Monogr. i. 100. Fischer, Ured. Schweiz, p. 232. McAlpine,

Rusts of Australia, p. 159, f. 62—3.

Uredospores. Sori amphigenous or on the stems, generally on minute spots, scattered, pulverulent, cinnamon, *primary* sori rather large, *secondary* minute; spores globose to ellipsoid, echinulate, brown, $22-28\ \mu$, with two germ-pores.

Teleutospores. Sori similar, but punctiform (chiefly and larger on the stems), black; spores ellipsoid to ellipsoid-obovate, rounded at both ends or rarely attenuated downwards, not thickened above, hardly constricted, delicately verruculose-punctate (?), brown, $30-46 \times 18-24\ \mu$; epispore thin; pedicels hyaline, short.

On *Hypochoeris radicata*. Not uncommon. July—September. The records from other countries include all the three British species of *Hypochoeris*. Only uredospores were seen in British specimens. (Figs. 100, 101.)



Fig. 100. *P. Hypochoeridis*.
Uredospore (British) on
H. radicata.

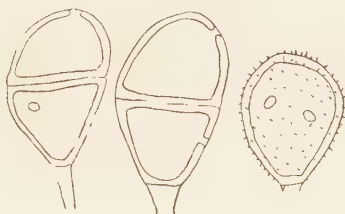


Fig. 101. *P. Hypochoeridis*. Teleuto-
spores and uredospore, on *H. glabra*
(Berlin, ex herb. Sydow).

This species, which has been often stated to be a *Brachypuccinia*, differs from most others of the type of *P. Hieracii* in having two kinds of uredo-sori—the *primary* ones 1—2 mm. wide, and only on the leaves, the *secondary* ones conspicuously smaller, almost punctiform. In this respect it approaches *P. Cyani* and *P. obtegens*, but Jacky showed that in his cultures it did not produce spermogones (Centralbl. f. Bakter. 1907, xviii. 83), as they do. The alleged punctations of the teleutospores were invisible in all the specimens I have seen.

DISTRIBUTION: Europe, Siberia, North America, Chili, Australia.

24. *Puccinia Leontodontis* Jacky.

Puccinia Hieracii Plowr. Ured. p. 184 p.p.

P. Leontodontis Jacky, Composit.-Puccin. p. 75. Sydow, Monogr. i. 114. Fischer, Ured. Schweiz, p. 231, f. 182.

Uredospores. Sori amphigenous, but chiefly hypophyllous, scattered, not confluent, minute, punctiform, surrounded by the cleft epidermis, cinnamon; spores globose to ellipsoid, echinulate, brown, 25—32 μ diam. or 27—35 $\times$ 24—27 μ , always with two opposite germ-pores above the equator.

Teleutospores. Sori similar, but darker-brown; spores variable, ellipsoid to oblong or obovate, rounded at both ends, not thickened above, not constricted, delicately verruculose or

faintly granulated, chestnut-brown, $30-42 \times 21-27 \mu$; epispore thin; pedicels hyaline, short or nearly as long as the spore.

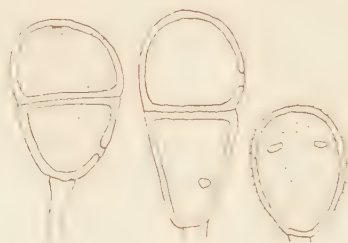


Fig. 102. *P. Leontodontis*. Teleutospores and uredospore, on *L. autumnalis*.

On *Leontodon autumnalis*, *L. hispidus*. August, September. Not uncommon. (Fig. 102.)

The teleutospores of this species are said to be more than usually variable; sometimes the sori, according to Sydow, are seated on coloured spots, but more often the spots are wanting. Up to the present, no experimental cultures appear to have been carried out with this *Puccinia*, and it is separated from *P. Hieracii* mainly because it is parasitic upon a different genus. I have found it mostly upon old yellowing leaves.

DISTRIBUTION: Europe generally.

25. *Puccinia Tragopogi* Corda.

Æcidium Tragopogi Pers. Syn. p. 211.

Æ. Tragopogonis Cooke, Handb. p. 537; Micr. Fung. p. 195, pl. 1, f. 1—3.

Puccinia Tragopogi Corda, Icon. v. 50. Plowr. Ured. p. 197. Sacc. Syll. vii. 668 p.p. Sydow, Monogr. i. 167. Fischer, Ured. Schweiz, p. 215, f. 166.

P. sparsa Cooke, Handb. p. 498; Micr. Fung. p. 205.

Spermogones. Epiphyllous, honey-coloured, sometimes absent.

Æcidiospores. *Æcidia* hypophyllous, without spots, scattered uniformly over the whole surface, and on other green parts, cup-shaped, with a white torn revolute margin; spores globose to ellipsoid, densely verrucose, pale-orange, $20-30 \times 18-24 \mu$, with three germ-pores.

Teleutospores. Sori amphigenous, without manifest spots, scattered, occasionally aggregated, minute, punctiform, long covered by the epidermis, at length pulverulent, dark-brown; spores ellipsoid, rounded at each end, not thickened above, gently constricted, tuberculate, chestnut-brown, $26-45 \times 18-32 \mu$; pedicels hyaline, short.

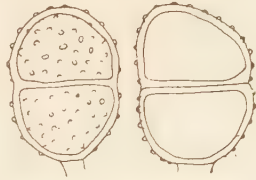


Fig. 103. *P. Tragopogi*.
Teleutospores.

On *Tragopogon pratensis*. Not uncommon. April—September. (Fig. 103.)

The mycelium arising from the infection of young plants by the basidiospores permeates the whole of the host, so that æcidia are produced on every part—stems, leaves, bracts, and receptacles—and the infected plants are noticeable for their paler colour and distorted form. It is believed to hibernate also in the upper part of the root-stock. The mycelium of the teleuto-sori is, on the contrary, strictly localised. Uredospores are not produced in separate sori, but a few can be found intermixed with the teleutospores, as well as a few mesospores; the former can be distinguished from the latter by being delicately aculeate, not tuberculate. The teleutospores of this species are grossly and distinctly warted, reminding one of those of *Uromyces tuberculatus*; they can be found at the same time as the æcidia, but are much rarer, or at least less frequently observed.

DISTRIBUTION: Europe, Asia Minor.

26. *Puccinia Chondrillæ* Corda.

Æcidium Prenanthis Pers. Syn. p. 208 (*non* Cooke, Handb. p. 542; Micr. Fung. p. 198).

Puccinia Chondrillæ Corda, Icones, iv. 15. Fischer, Ured. Schweiz, p. 200, f. 156.

P. Prenanthis Auct. p.p.; Plowr. Ured. p. 148. Sydow, Monogr. i. 106. McAlpine, Rusts of Australia, p. 162 (?).

Æcidiospores. Æcidia hypophyllous or on the petioles, rarely a few on the upper surface, seated on large yellow and purple spots, in clusters as much as 6—8 mm. broad, at first hemispherical, opening by a pore, then flattened, whitish or yellow, sometimes with a purplish tinge; spores globose to ellipsoid, delicately verruculose, pallid-orange, $13-24 \mu$; peridium poorly developed.

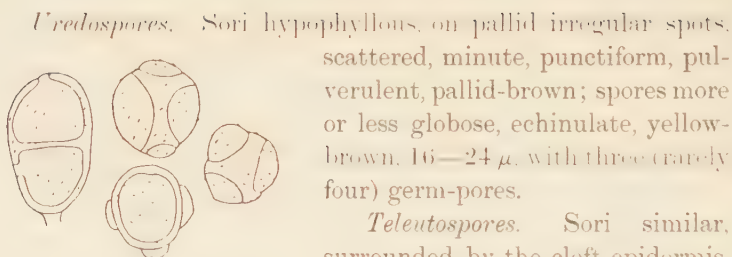


Fig. 104. *P. Chondrilla*. Teleutospore and uredospores.

Uredospores. Sori hypophyllous, on pallid irregular spots, scattered, minute, punctiform, pulverulent, pallid-brown; spores more or less globose, echinulate, yellow-brown, $16-24\ \mu$, with three (rarely four) germ-pores.

Teleutospores. Sori similar, surrounded by the cleft epidermis, blackish-brown; spores ellipsoid, rounded and not thickened above, not constricted, rounded below, very delicately verruculose, brown, $26-36 \times 16-24\ \mu$; pedicels hyaline, very short.

On *Lactuca (Prenanthes) muralis* only. Not common. April—September. All three spore-forms may be found on the same leaf. (Fig. 104.)

The æcidium of this species is not provided with a proper peridium and opens with a pore, never assuming the form of a cup; moreover the æcidiospores are more round than angular. The germ-pores of the uredospores are covered with a broad convex colourless cap, which swells up somewhat in water. The genetic connection of the three spore-forms has been proved experimentally by Jacky (Centralbl. f. Bakt. ix. 1902, p. 842), as also the fact that the parasite is not transmissible to other species of *Lactuca*. There is another æcidium also found on *Lactuca muralis* on the continent which possesses a well-developed peridium; this belongs to *Puccinia Opizii* Bubák, and has its teleutospores on *Carex muricata*.

DISTRIBUTION: Europe generally.

27. *Puccinia variabilis* Grev.

Æcidium Grevillei Grove, Journ. Bot. 1886, p. 129.

Puccinia variabilis Grev. Scot. Crypt. Fl. pl. 75. Cooke, Handb. p. 500; Micr. Fung. p. 207, pl. 4, f. 82—3. Plowr. Ured. p. 150. Sydow, Monogr. i. 163. Fischer, Ured. Schweiz, p. 202, f. 158.

Æcidiospores. Æcidia amphigenous, on minute indeterminate yellow or purplish spots, solitary or a few loosely aggregated, cup-shaped, with whitish torn margin; spores subglobose or ovate, with orange contents, verruculose, $20-25 \times 15-20\ \mu$.

Uredospores. Sori amphigenous, on very minute yellow or

purplish spots, scattered, minute, punctiform, soon naked. brown; spores few, globose to ovate, echinulate, brown, $22-32 \times 19-26 \mu$, with two germ-pores.

Teleutospores. Sori similar, but darker; spores ellipsoid to oblong, rounded at both ends, not thickened above, not con-



Fig. 105. *P. variabilis*. Aecidia, on leaf of *Taraxacum*, and teleutospore.

stricted, delicately verruculose, brown, $28-40 \times 18-25 \mu$; episporium thin; pedicels hyaline, about as long as the spore, but deciduous.

On *Taraxacum officinale* and its variety *palustre*. July—October. Not common. (Fig. 105.)

Plowright and Soppitt both proved, by laying leaves affected with the aecidium of this species on healthy plants of *Taraxacum*, that the uredo- and teleutospores were produced in about fourteen days. In July the three spore-forms may be found on the same leaf.

There are two forms of aecidium found upon *Taraxacum*; one, *Aecidium Grevillei* Grove (= *Æ. Taraxaci* Grev. non K. et S.), spreads pretty uniformly over the whole leaf in "numerous little clusters with single ones scattered between them," as Greville describes it (Flor. Edin. p. 444)—the other, *Æ. Taraxaci* K. et S., forms large round clusters, and belongs to *P. silvatica*. Fischer points out that the two aecidia differ in the form of their peridium cells, those of *P. variabilis* having the membrane thickened on the inner side, while those of *P. silvatica* have the outer wall most strongly thickened. He states, furthermore, that it will be found that this difference is characteristic in general of autæcious and heteræcious species respectively. It is not, however, universally so, e.g. the aecidium of *P. albescens* has the outer wall much more strongly thickened, although it is autæcious.

Greville figures the teleutospores of his species (Scot. Crypt. Flor. pl. 75) as having either one or both of the cells sometimes divided by a vertical septum.

DISTRIBUTION: Switzerland, Sweden.

28. **Puccinia Taraxaci** Plowr.

Puccinia Phaseoli var. *Taraxaci* Rebent. Fl. Neomarch. p. 356.

P. variabilis Grev. ; Cooke, Handb. p. 500 ; Micr. Fung. p. 207 p.p.

P. Taraxaci Plowr. Ured. p. 186. Sacc. Syll. ix. 305. Sydow, Monogr. i. 164. Fischer, Ured. Schweiz, p. 226, f. 178.

Spermogones. In little yellow roundish clusters.

Uredospores. Sori amphigenous, with or without spots, scattered, minute, sometimes confluent and larger, roundish or oblong, pulverulent, brown; spores globose to ovate, echinulate, pale-brown, $22-27 \times 16-24 \mu$, with two germ-pores.



Fig. 106. *P. Taraxaci*.
Teleutospore and uredospore.

Teleutospores. Sori similar, but blackish, $\frac{1}{2}-\frac{3}{4}$ mm. diam.; spores ellipsoid to ovate, rounded at both ends, not thickened above, not constricted, very delicately verruculose, brown, $25-38 \times 16-24 \mu$; episporium thin; pedicels hyaline, short.

On *Taraxacum officinale*. Rather common. Spermogones and primary uredospores in April; the teleutospores may be found till November. The distinctions which Plowright attempts to draw between the primary and secondary uredospores are not so marked as is the case in *P. Centaureae*, and break down in practice. (Fig. 106.)

This species differs from *P. variabilis*, with which it was formerly confused, chiefly in the absence of the æcidium. But, in addition to that, the uredospores of *P. Taraxaci* are far more abundant and the sori more especially found on the upper leaf-surface; the uredospores of *P. variabilis* are scanty and are usually intermixed in the teleuto-sori. *P. Taraxaci* is morphologically indistinguishable from *P. Hieracii*, but culture experiments have proved that it cannot be transferred from *Taraxacum* to the allied genera of the Compositæ.

Plowright's remark (*l. c.* p. 187) that I considered this species to have "a true æcidium" is a mistake, arising probably from a confusion between it and *P. variabilis*.

DISTRIBUTION: Europe, North America, Japan, East Indies.

29. **Puccinia Sonchi** Rob.

Æcidium Sonchi Johnst. ; Plowr. Ured. p. 266.

Puccinia Sonchi Rob. in Desm. Ann. Sci. Nat. ser. 3, xi. 274. Grove, Sci. Gossip, 1885, p. 9, f. 6—9. Plowr. Ured. p. 196. Sacc. Syll. vii. 638. Sydow, Monogr. i. 154.

[*Spermogones*. Obtained artificially on *S. arvensis* by Tranzschel.]

Uredospores. Sori generally hypophyllous, on the stem collected in small oblong patches 4—5 mm. long, on yellowish spots, scattered or gregarious, minute, at first covered by the epidermis which is raised over them in a hemispherical vesicle, then pierced at the top but never widely open, yellowish, surrounded by a dark-brown line of paraphyses; spores more or less oblong or obovate, densely verrucose, with a very thick episore, contents oily, yellowish, $24\text{--}38 \times 15\text{--}21 \mu$.

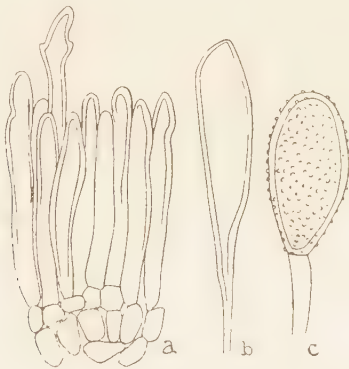


Fig. 107. *P. Sonchi*. a, the line of dark-brown paraphyses surrounding the uredo-sori; b, a pale-brown paraphysis; c, a uredospore; all on *S. oleraceus*. $\times 600$.

[*Teleutospores*. Sori hypophyllous, rarely on the stems, on irregular brownish spots, more compact, rounded-pulvinate, scattered or aggregated, confluent when on the stem, covered by the epidermis, black; spores ovate or oblong, rounded or truncate (rarely attenuated) above, thickened ($3\text{--}8 \mu$), constricted, rounded below, smooth, pale-brown, $30\text{--}60 \times 20\text{--}30 \mu$; pedicels somewhat long, brownish, persistent; mesospores ovate,

clavate, or oblong, thickened at the apex, brownish, $45-60 \times 20-25 \mu$: paraphyses numerous, reddish-brown, clavate and somewhat thickened at the apex.]

On *Sonchus arvensis*, *S. asper*, *S. oleraceus*. Uredospores only seen, July—September. Rather rare. (Fig. 107.)

In Sydows' Monographia this species is said to be confined to the neighbourhood of the coast or nearly so. It has been recorded by Prof. Trail at Aberdeen, by Mr Johnston at Berwick-on-Tweed, by Mr D. A. Boyd from Ayrshire; also from Sutton, near Askern, and Mulgrave Woods in Yorkshire; I have received specimens from Mr Hawkes collected near Birmingham, from Mr Phillips near Hull, from Mr T. B. Roe near Scarborough, and from Mr J. Adams at Howth, Co. Dublin, and Westport, Co. Mayo.

It is a remarkable species, and worthy of close investigation. Though the uredo is sometimes confounded with *Coleosporium Sonchi*, it is readily distinguished by its brown paraphyses which form only a single row round the sori and are easily seen with a lens through the epidermis as a dark line surrounding the yellow spore-layer. It resembles at first sight an æcidium, and has been more than once described as such: but it opens by a pore the edges of which do not curl back. The so-called paraphyses are really the upper part of a delicate imperfect peridium, composed of hyaline pseudo-parenchyma (cells $5-10 \mu$ diam.); at the top these cells become elongated, linear, parallel, at first colourless, then brownish and more or less clavate, and finally very dark brown, subopaque and irregular. This colour is retained for many years in the dried specimens, though the spores are bleached. The peridium resembles in some respects that which surrounds the uredo-sori of *Melampsorella Caryophyllacearum*. The spores themselves are at first sight like æcidiospores, with thick colourless walls, and yellowish contents, the sculpture resembling that of the æcidiospores of *Endophyllum*. Ultimately the wall becomes thinner and brownish; the spores are borne singly on pedicels, like ordinary uredospores.

Tranzschel (Ann. Mycol. 1909, vii. 182) sowed the teleutospores on *S. arvensis* and obtained spermogones, followed by the uredospores. This species is widely different from a typical *Puccinia*.

DISTRIBUTION: Western Europe, Algeria, Canaries, Japan.

30. *Puccinia Crepidis* Schröt.

Puccinia Crepidis Schröt. Pilze Schles. p. 319. Sacc. Syll. vii. 607.

Sydow, Monogr. i. 64. Fischer, Ured. Schweiz, p. 207, f. 163.

[*Spermogones*. Scattered amongst the æcidia, nearly always present, in little clusters of 6—10, brownish.

Æcidiospores. *Æcidia* hypophyllous, evenly spread over the whole leaf-surface, flat, with white margin; spores delicately verruculose, yellowish, $15-25 \times 14-20 \mu$.]

Uredospores. Sori amphigenous, minute, roundish, scattered, surrounded by the epidermis, cinnamon; spores globose to ovoid, delicately aculeate, brown, $20-24 \times 16-20 \mu$, with two or three germ-pores.

Teleutospores. Sori hypophyllous, rarely also epiphyllous, minute, long covered by the epidermis, blackish-brown; spores ellipsoid to ovoid, rounded at both ends, not thickened above, scarcely or not at all constricted, very delicately punctate (?), chestnut-brown, $20-30 \times 17-22 \mu$; epispore thin; pedicels hyaline, very slender.

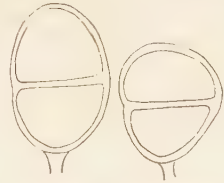


Fig. 108. *P. Crepidis*.
Teleutospores (Antrim).

On *Crepis virens*. Rare. August. (Fig. 108.)

This species seems to be very rare. It is recorded for Scotland (Moray, Rev. Jas. Keith) in Scot. Nat. 1884, p. 270, and I have a specimen showing teleutospores from Ireland (J. Adams), but I have not seen the *æcidia* on British specimens. The punctations were not discernible on the teleutospores.

DISTRIBUTION: Central Europe.

31. *Puccinia major* Dietel.

Æcidium Compositarum var. *Prenanthis* Cooke, Handb. p. 542; Micr. Fung. p. 198.

Puccinia Lapsanae Plowr. Ured. p. 149 p.p.

P. major Dietel, Mitth. Thür. Bot. Ver. 1894, heft vi. Sacc. Syll. xiv. 310. Sydow, Monogr. i. 66. Fischer, Ured. Schweiz, p. 214.

Spermogones. Generally hypophyllous, on reddish or yellowish spots.

Æcidiospores. *Æcidia* hypophyllous, often surrounding the spermogones, on the same thickened spots, in roundish clusters or more often forming oblong patches on the nerves and petioles; shortly cylindrical, with white torn erect margin; spores ovoid or rarely subglobose, delicately verruculose, orange, $20-30 \times 16-24 \mu$.

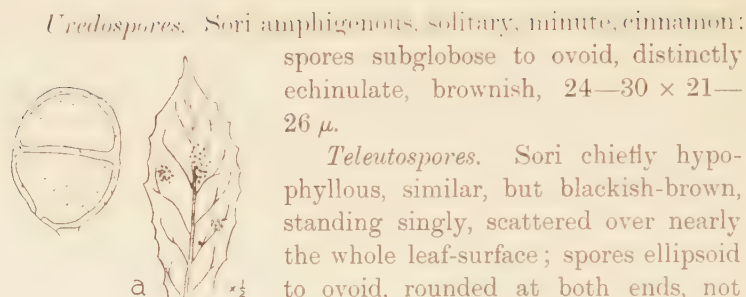


Fig. 109. *P. major*. Teleutospore, on *C. paludosa*; a, æcidia on leaf of same, $\times \frac{1}{2}$.

Uredospores. Sori amphigenous, solitary, minute, cinnamon: spores subglobose to ovoid, distinctly echinulate, brownish, $24-30 \times 21-26 \mu$.

Teleutospores. Sori chiefly hypophyllous, similar, but blackish-brown, standing singly, scattered over nearly the whole leaf-surface; spores ellipsoid to ovoid, rounded at both ends, not thickened above, hardly constricted, very delicately verruculose, chestnut-brown, $33-48 \times 22-30 \mu$; epispore thin; pedicels short, deciduous.

On *Crepis paludosa*. Æcidia in June; uredospores, mixed with teleutospores, August and September. Yorkshire (Soppitt), Braemar (Trail), Dolgelly, Wales, and in Ireland. (Fig. 109.)

This species was formerly considered a variety (*major*) of *P. Lapsanæ* on account of the larger spores, but is now kept separate. Dietel proved by cultures that the uredo- and teleutospores are connected with the æcidial generation. From *P. Crepidis*, on *Crepis virens*, it is said to be distinguished, not only by the size of the spores, but also by the difference in the way in which the æcidia occur on the leaves; the minute, black, solitary teleuto-sori seem also different.

DISTRIBUTION: Northern and Central Europe.

32. *Puccinia Hieracii* Mart.

Uredo Hieracii Schum. Enum. Pl. Säll. ii. 232.

Trichobasis Hieracii Cooke, Micr. Fung. p. 224 p.p.

Puccinia Hieracii Mart. Fl. Mosquen. p. 226. Cooke, Micr. Fung. p. 207 p.p. Plowr. Ured. p. 184, p. min. p. Sacc. Syll. vii. 633 p.p. Sydow, Monogr. i. 95. Fischer, Ured. Schweiz, p. 230, f. 181.

Spermogones. In little yellowish clusters on leaves and stems.

Uredospores. Sori amphigenous, usually epiphyllous, on pale spots which are sometimes hardly perceptible, scattered, scarcely confluent, minute, punctiform, soon naked, pulverulent,

cinnamon; spores globose to ellipsoid, echinulate, yellow-brown, $24-29 \times 16-25 \mu$, with two germ-pores.

Teleutospores. Sori similar and often on the stems, but dark-brown; spores ellipsoid or somewhat ovate, rounded and not thickened above, scarcely constricted, usually rounded below, very delicately verruculose, brown, $25-40 \times 16-24 \mu$; epispore thin; pedicels hyaline, usually very short.

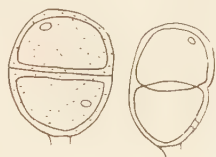


Fig. 110. *P. Hieracii*.
Teleutospores.

On leaves and stalks of *Hieracium*, *H. boreale*, *H. murorum*, *H. Pilosella*, *H. umbellatum* and various subspecies. Very common. May—November. (Fig. 110.)

It was proved by Jacky that this species, which occurs so abundantly on *Hieracium*, cannot be transferred to other genera of Compositæ. As a similar fact has been demonstrated for many other species of Uredinales, there is sufficient ground for the assumption, now generally made, that most species of *Puccinia*, etc., which are parasitic on different genera should be regarded as distinct, even when no experimental evidence exists in favour of that course. Jacky was also inclined to suspect that *P. Hieracii* might hereafter be divisible into a number of biologic races, of which, however, he only indicated one, that on *H. villosum* belonging to the section *Pilosella*. René Probst (Centralbl. f. Bakt. 1909, 2. xxii. 676) not only divided *P. Hieracii* into 13 biologic races, arranged under two subspecies, *P. Piloselloidarum* on the section containing *H. Pilosella* and its allies, and *P. Hieracii* (sens. strict.) on the other species, forming the section *Euhieracium*,—but he goes on to reduce the question of such races to an absurdity by “proving” that one of them was restricted to a mere form of a variety of a subspecies (*Hieracium Pilosella*, subsp. *vulgare*, var. *genuinum*, forma *subpilosum*).

The two subspecies may perhaps be defensible, if they are distinguished morphologically, as Probst states, by the fact that in *P. Piloselloidarum* the germ-pores of the uredospore are strictly equatorial, but in *P. Hieracii* they are removed towards the upper pole.

DISTRIBUTION: Europe, Asia Minor, North America, Chili.

33. *Puccinia Campanulæ* Carm.

Puccinia Campanulæ Carmich. in Berk. Engl. Fl. v. 365. Cooke, Handb. p. 498; Micr. Fung. p. 205. Plowr. Ured. p. 200. Sacc. Syll. vii. 677. Sydow, Monogr. i. 196, f. 182. Fischer, Ured. Schweiz, p. 175, f. 136.

Teleutospores. Sori hypophyllous, rarely epiphyllous, often on the petioles and stems, scattered or circinate, minute, sometimes (especially on the stems) confluent and larger, long covered by the epidermis, then surrounded by it, roundish or irregular, ferruginous-brown; spores ellipsoid or oblong, rounded and not thickened above, but with a pale papilla to each germ-pore, constricted, rounded or somewhat attenuated below, smooth, pale-brown, 26—

Fig. 111. *P. Campanulae*. Teleutospores, on *C. rotundifolia*.

45 $\times$ 12—22 μ ; pedicels hyaline, thin, deciduous, as long as the spore or shorter.

On *Campanula Rapunculus*, *C. rotundifolia*. Not common. June—August. (Fig. 111.)

According to Sydow, the statement in Cooke's Handbook that *Jasione montana* is one of the hosts of this species is entirely without corroboration and is probably due to an error in the determination of the plant: the statement is copied from the notice in Berk. Ann. Nat. Hist. ser. 2, v. 462—"On *Jasione montana*, Lampeter, *J. Ralfs*." Fischer mentions that he has occasionally met with one-celled teleutospores, which I have not seen.

DISTRIBUTION: Central Europe.

34. **Puccinia Adoxæ** Hedw. f.

Aecidium Adoxæ Opiz, in Kl. Herb. Myc. i. no. 780.

Puccinia Adoxæ Hedw. in DC. Flor. fr. ii. 220. Cooke, Micr. Fung. p. 209 p.p. Plowr. Ured. p. 207. Sacc. Syll. vii. 612. Sydow, Monogr. i. 203 p.p. Fischer, Ured. Schweiz, p. 146, f. 111.

P. Saxifragarum Schl.; Cooke, Handb. p. 506 p.p. W. G. Smith, in Gard. Chron. xxiv. (1885), p. 21, f. 7.

Teleutospores. Sori roundish, united in large clusters, often confluent, on discoloured spots on the leaves, or on the petioles forming elongated swollen patches, long covered by the silver-grey epidermis, at length naked, pulverulent, dark-brown; spores ellipsoid to broadly fusiform, rounded or attenuated above, with a conspicuous colourless papilla, mostly rounded below, scarcely constricted, smooth, chestnut-brown, 28—42 $\times$ 14—21 μ ; pedicels hyaline, delicate, short, deciduous.

On *Adoxa Moschatellina*. March—May. Not uncommon. All parts of the plant are affected, rhizomes, petioles, leaves, peduncles and flowers. (Fig. 112.)

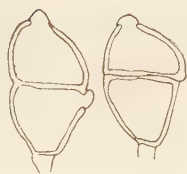


Fig. 112. *P. Adoxae*.
Teleutospores.

Puccinia Adoxae and the æcidium of *P. albescens* (q.v.) are about equally common, but are rarely found together; they occur not only on different plants, but usually also in widely separated localities. In fact, it is agreed by all observers that there are three cases, (1) where the æcidium alone occurs, (2) where the teleutospores alone occur, and (3) where they both occur together; in the latter case uredospores are found with the teleutospores in the same sorus. The first is considered to be the æcidium of *P. argentata* (q.v.), the second is *P. Adoxae*, and the third is *P. albescens*.

Soppitt first proved that the teleutospores of *P. Adoxae*, laid upon healthy plants when in active germination after passing the winter, reproduce the teleutospores in about ten days without the intervention of other spore-forms. It is therefore a Micropuccinia. Whether the wide-spreading mycelium is perennial or not is uncertain. Worth. G. Smith raised seedlings of *Adoxa* from berries of an infected plant; the seedlings exhibited the *Puccinia* from the earliest stages of growth, but we are not told what precautions were taken to prevent infection from outside. He also found (*l.c.*) teleuto-sori, in a state of nature, on fusiform swellings of the underground parts of the plant (peduncles and petioles), as also on rhizomes and scales, in March; the spores were irregular, one-, two-, or three-celled. In April the leaves, and in May the flowers and young fruits were infected. No mycelium could be found in the rhizome. If Plowright's ascription of a perennial mycelium is incorrect, the infection must have first taken place, in this instance, underground on the young growth, and the mycelium gradually spread upwards. That this is probably the case is shown by Fischer's experiment; he kept plants which had borne teleutospores in pots—if he removed all the leaves, they produced healthy growth next spring, whereas, if the leaves were left on and allowed to fall upon the soil, one plant at least (out of four) showed teleutospores on the new shoots. Bubák inclines to the same opinion (*Centralbl. f. Bakt.* 2. xvi. 150).

As will be seen from the synonymy, *P. Adoxae* and *P. albescens* are united (under the former name) in Sydows' *Monographia*, while Soppitt, Plowright, Bubák and Fischer consider them distinct. In any case they are very closely allied; the probability is that *P. Adoxae* is a mutation from *P. albescens* which has acquired the habit of reproducing teleutospores from teleutospores directly, while the original species from which it was evolved still maintains all the three spore-forms, though two of them are

rarely observed. I have pointed out elsewhere that it is on spring flowering plants of this kind that *Micropucciniae* would naturally arise (as well as on alpine plants), if they are the result of an adaptation to a shortened vegetative period. *Uromyces Fauriae* may be taken as another instance of a similar character.

35. *Puccinia albescens* Plowr.

Aecidium albescens Grev. Fl. Edin. p. 444. Cooke, Handb. p. 536 ;
Micr. Fung. p. 194.

Puccinia albescens Plowr. Ured. p. 153. Fischer, Ured. Schweiz,
p. 144, f. 110.

P. Adoxae Hedw. ; Cooke, Micr. Fung. p. 209 p.p. Sacc. Syll. vii.
612 p.p. Sydow, Monogr. i. 203 p.p.

Spermogones. Scattered among the aecidia, yellowish.

Aecidiospores. Scattered uniformly over the whole surface of the leaves, also on the petioles, shortly cylindrical, whitish-yellow, with a deeply cut revolute margin; spores finely warted, pale-yellowish, $15-22\mu$.

Uredospores. Sori minute, scattered singly or in little clusters, soon naked, brown; spores globose to ellipsoid, echinulate, pale-brown, $21-28 \times 18-25\mu$, with two germ-pores.

Teleutospores. Sori similar, or teleutospores at first in the same sori as the uredospores; spores ellipsoid to subfusiform, rounded or attenuated above, with a conspicuous colourless papilla, usually more or less rounded below, hardly constricted, smooth, chestnut-brown, $32-45 \times 14-25\mu$; pedicels hyaline, delicate, short, deciduous.



Fig. 113. *P. albescens*.
Teleutospores.

On *Adoxa Moschatellina*. The aecidia appear in April or even in March, uredo- and teleutospores in May and June. Apparently not uncommon in the aecidium stage, which makes the affected leaves paler and dwarfed; but see the following paragraphs. (Fig. 113.)

The uredo- and teleutospores seem to be rare in a natural state, although Schroter, Nielsen, Soppitt and Fischer have all produced them in small quantity artificially from the aecidiospores; the latter laid affected

leaves on healthy plants on the 26th of April, removing them after a time; nevertheless the experimental plants showed both uredo- and teleutospores on May 16th. Their mycelium is localised, but that of the æcidium permeates the whole plant; it is a disputed point whether it perennates in the rhizome or not; Plowright affirms, Fischer denies this, and Bubák thinks it probably not perennial (*Centralbl. für Bakt.* 2. xvi. 150). Fischer records and figures abnormal three- or four-celled teleutospores.

The distinctions between this species and *P. Adoxæ* lie not only in the presence of the æcidium and uredo, but also in the appearance and character of the teleuto-sori. In *P. albescens* these are widely scattered and mostly single, and only follow the æcidium towards the end of May—in *P. Adoxæ* they are crowded in larger groups, on more or less deformed parts of the plant, and can be found as early as April or even March; moreover there are no uredospores in them.

An æcidium on *Adoxa* is found in North America, but it has been said (Dietel, 1895) that teleutospores have only once been seen there on that host. On that account Dietel considers that the æcidium is able to reproduce its own spore-form. This is contradicted by Bubák's experiments and, since *P. argentata* is common in North America, it is more probable that the æcidium on *Adoxa* found there is not *Æcidium albescens*, but belongs to *P. argentata*. Bubák, in fact, considers that this is the case with most of the records of *P. albescens*. He says that the æcidium of *P. argentata* has golden-yellow spores, and that he has met with the true *Æcidium albescens* only from Yorkshire and Baden. I do not quite share this view: I have found teleutospores, apparently not mixed with uredospores, in mid-April, on the same plant on which were abundant æidia with golden-yellow spores. There are three possible explanations of this occurrence: either (1) it was *P. albescens* with deep-coloured spores, or (2) there were on the same plant *P. Adoxæ* and the æcidium of *P. argentata* (which is a very rare species in Britain), or (3) all the distinctions usually given must be upset. Which is the true explanation, future experiments alone can decide.

36. *Puccinia Asperulæ-odoratæ* Wurth.

Puccinia Asperulæ Eckl. Symb. Myc. p. 56 p.p.

P. punctata Lk.; Sydow, Monogr. i. 213 p.p.

P. Galii Plowr. Ured. p. 143 p.p. Fischer, Ured. Schweiz, p. 332, f. 246 (see *ibid.* p. 555).

P. Asperulæ-odoratæ Wurth, Centralbl. f. Bakter. 2. xiv. 314, f. 9—10.

Æcidiospores. *Æcidia* hypophyllous, in little clusters, surrounded by a paler zone, cup-shaped, with a slightly projecting

white margin; spores with a thin, colourless, faintly warted membrane, 14—21 μ .

Uredospores. Sori mostly hypophyllous, roundish, scattered or in minute clusters, on the stems linear, soon naked, clear chocolate-brown; spores globose to pyriform, brown, finely echinulate, 18—30 μ , with two mostly equatorial germ-pores.

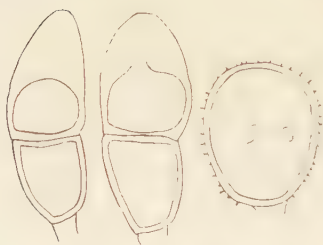


Fig. 114. *P. Asperulae-odoratae*.
Teleutospores and uredospore.

Teleutospores. Sori similar, but long covered by the epidermis; spores ellipsoid to clavate, rounded or conical above and thickened (up to 7 μ or more), distinctly con-

stricted, tapering below, smooth, clear brown, 30—52 $\times$ 17—21 μ ; pedicels short.

On *Asperula odorata*. Rare. (Fig. 114.)

Distinguished by Wurth from *P. punctata* on the ground of cultures: the teleutospores have, he says, a less thick cap, which is pale at the apex, and the uredospores have only two germ-pores. Description mainly after Fischer and Wurth, and not agreeing exactly with my specimens; the species is hardly distinguishable, however, from *P. punctata*. Fischer figures also three-celled teleutospores.

37. *Puccinia punctata* Link.

Aecidium Galii A. et S. (non Pers.); Cooke, Handb. p. 540; Mier.

Fung. p. 196, pl. 2, f. 15—17.

Trichobasis Galii Lév.; Cooke, Mier. Fung. p. 226 p.p.

Puccinia punctata Link, Obs. Myc. ii. 30 (1816). Sydow, Monogr. i. 213 p.p.

P. Galii Schw. Syn. Fung. Carol. p. 73 (1822). Plowr. Ured. p. 143 p.p. Sacc. Syll. vii. 600. Fischer, Ured. Schweiz, pp. 332, 554, f. 243—5.

P. Galiorum Link, Sp. Pl. ii. 76 (1825). Cooke, Handb. p. 501; Mier. Fung. p. 208, pl. 8, f. 172—3 p.p.

Spermogones. Amphigenous, in little clusters, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous, scattered or collected in orbicular clusters on roundish or oblong paler spots, slightly cylindrical, with a short white recurved margin; spores globose or broadly ellipsoid, orange-yellow, somewhat smooth, $16-23\ \mu$.

Uredospores. Sori hypophyllous, minute, roundish, on the stems linear, reddish-brown, often confluent; spores globose to ovate, aculeolate, pale-brown, $22-30 \times 17-23\ \mu$, with two or three germ-pores.

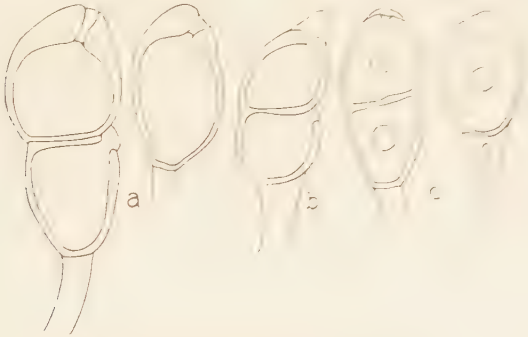


Fig. 115. *P. punctata*. Teleutospores; a, on *G. saxatile*; b, on *G. palustre*; c, on *G. verum*.

Teleutospores. Sori similar, but black, compact, and persistent; spores ellipsoid to clavate, truncate, rounded or conically attenuate above, where they are much thickened (up to $14\ \mu$), and often darker, slightly constricted, tapering below, brown, smooth, $30-56 \times 14-24\ \mu$; pedicels brownish above, persistent, thick, about as long as the spore; a few mesospores occasionally.

On leaves and stems of *Galium Cruciata* (?), *G. Mollugo*, *G. palustre*, *G. saxatile*, *G. uliginosum*, *G. verum*. Not uncommon. *Æcidia*, June; teleutospores, August and September. (Fig. 115.)

The forms of *P. punctata* on these various species of *Galium* differ considerably in the shape and size of the teleutospores, and have been divided into several biological races. On *G. Aparine* there is a distinct species, *P. difformis* (q.v.); but it is possible that *P. punctata* also occurs

on that plant. I am not certain that *P. punctata* lives on *G. Cruciata*, though I think I have seen it on that host; the two usual species on that *Galium* are *P. Celakovskyana* and *P. Valantiae* (q.v.).

The æcidium seems to be less common than the other spore-forms: I have seen it on *G. Mollugo*, *G. verum* and *G. uliginosum*. Mesospores have been observed on *G. palustre*, *G. saxatile* and *G. verum*. On *G. saxatile* the teleutospores were slightly larger than in the normal form, but otherwise identical; *P. Valantiae*, which occurs on that same host, is easily distinguishable.

DISTRIBUTION: Europe, Siberia, North America, Chili.

38. *Puccinia Celakovskyana* Bubák.

Puccinia Celakovskyana Bubák, Ber. Böhm. Ges. Wissen. Prag, 1898, p. 11. Wurth, Centralbl. f. Bakt. pt. 2, xiv. 212, 310, f. 2—3. Sacc. Syll. xvi. 287. Sydow, i. 216. Fischer, Ured. Schweiz, p. 335, 555, f. 247.

Spermogones. Amphigenous, dark honey-coloured.

Uredospores. *Primary* sori surrounding the spermogones and on the same mycelium, more or less circinate, surrounded by a yellowish zone, long covered by the epidermis, dark-brown; *secondary*, amphigenous, minute, scattered, soon naked, pale chestnut-brown or pale cinnamon; spores globose to obovate, distinctly echinulate, brown, $21-33 \times 18-25 \mu$, with two nearly equatorial germ-pores.

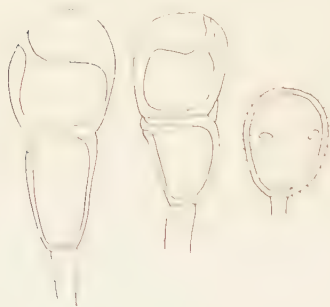


Fig. 116. *P. Celakovskyana*.
Teleutospores and uredospore.

Teleutospores. Sori hypophyllous, on brownish spots, thickly scattered, minute, roundish, on the stems linear and up to 1 mm. long, soon naked, pulvinate, black brown; spores oblong to clavate, rounded (very seldom narrowed) above where they are much thickened (up to 11μ) and darker, faintly constricted, tapering below, smooth, chestnut-brown, $35-56 \times 17-25 \mu$; pedicels hyaline, thick, persistent, not as long as the spore; an occasional mesospore is found.

On *Galium Cruciata*. Not uncommon. Uredospores, May—July; teleutospores, August, September. (Fig. 116.)

Distinguished at once from *P. Valantiae* on the same host by the dark colour of its teleutospores, and their very great and dark apical thickening. The presence of uredospores also distinguishes them; in *P. Celakovskyana* the two kinds of sori are often present together on the same leaf, the uredo-sori pale brown, and the teleuto-sori almost black.

According to Bubák, almost its only distinction from *P. punctata* lies in the absence of the æcidium whose place is taken by the primary uredo-sori. Wurth reports it also (*l.c.*) on *G. pedemontanum* on the continent, but demonstrated by culture-experiments that it could not be transferred to other species of *Galium*. Most of the records of *P. punctata* on *G. Cruciata* probably belong to this species, which certainly shows few morphological distinctions from the former; I find, however, that the teleuto-sori are larger, more numerous, and more compact in this species than in that found on *G. palustre*.

DISTRIBUTION: Central Europe.

39. *Puccinia Valantiae* Pers.

Puccinia Valantiae Pers. Obs. Myc. ii. 25. Cooke, Handb. p. 500;

Micr. Fung. p. 207. Plowr. Ured. p. 212. Sacc. Syll. vii. 685.

Sydow, Monogr. i. 217. Fischer, Ured. Schweiz, p. 336, f. 248.

P. acuminata Fekl.; Cooke, Micr. Fung. p. 208.

Teleutospores. Sori hypophyllous, rather thick, pulvinate, compact, orbicular, scattered, circinate or confluent, up to 2 mm. diam., at first yellowish-, then chestnut-brown, at length greyish-brown (from the spores germinating *in situ*), often elongated and causing distortion on the stems; spores fusoid or slightly oblong, attenuated at both ends, thickened (up to 9μ) above, somewhat constricted, smooth, pallid-brown, $35-65 \times 10-17\mu$; pedicels hyaline, persistent, up to 80μ long.

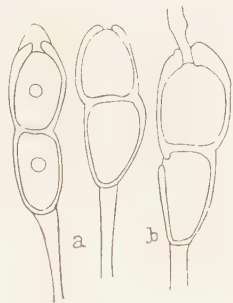


Fig. 117. *P. Valantiae*. Teleutospores; a, on *G. Cruciata*; b, on *G. saxatile*.

On *Galium Cruciata*, *G. saxatile*. June—September. Common. (Fig. 117.)

This Leptopuccinia is very distinct from *P. Celakovskyana*, which also lives on *G. Cruciata*, not only by the absence of uredospores, but also by

the fusiform shape, thin walls, and pale colour of the teleutospores, which often become totally devoid of thickening at the apex, by the dropping off of the pale thickening cap, on germination. *P. punctata* is additionally distinguished by the presence of the æcidium.

Fischer explains the fact, that distortions more usually accompany *P. Valantiae*, by the consideration that infection takes place from the basidiospores mainly through the cuticle of young and still growing parts, while teleuto-sori of *P. punctata* and *P. Celakovskyana* are produced by infection from spores whose germ-tubes can penetrate the stomata of parts of the plant which are already fully developed. The relations between the three species are very like those which subsist between *Uromyces Trifolii-repentis*, *U. Trifolii*, and *U. flectens*.

DISTRIBUTION: Europe, North America.

40. *Puccinia difformis* K. et S.

Puccinia difformis K. et S. Myk. Heft. i. 71 (1817). Cooke, Handb. p. 501; Micr. Fung. p. 208.

P. Galii Plowr. Ured. p. 144 p.p.

P. ambigua Lagh. in Sydow, Uredineen, no. 1056 (1897). Sacc. Syll. xvi. 288. Sydow, Monogr. i. 216.

Æcidiospores. Æcidia hypophyllous, on yellow spots, solitary or irregularly disposed over the whole leaf, whitish-yellow, with torn reflexed margin; spores verruculose, orange, 13–25 μ .

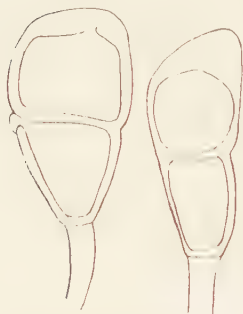


Fig. 118. *P. difformis*.
Teleutospores.

Teleutospores. Sori hypophyllous or on the stems, small, elliptic, solitary or clustered, on the stems often elongated and confluent, long covered by the ash-coloured epidermis, then naked, firm, black; spores ellipsoid to clavate, much thickened above, hardly constricted, tapering below, smooth, brown above, paler downwards, 35—

55 $\times$ 15—25 μ ; pedicels brownish, persistent, as long as the spore or longer.

On *Galium Aparine*. July—August. Surrey, Kent. (Fig. 118.)

The æcidia may be found together with the teleutospores right up to September, often on the same spot. This species is very different from the others on *Galium*; the teleuto-sori, as Cooke says, are "firm and compact like little spots of pitch," and may be accompanied by swellings and distortion. There are no uredospores.

DISTRIBUTION: Central and Northern Europe, India, North America.

41. **Puccinia Veronicæ** Schröt.

P. Veronicæ Schröt. Pilz. Schles. p. 347. Plowr. Ured. p. 211 p.p.
Sydow, Monog. i. 256. Fischer, Ured. Schweiz, p. 323, f. 235.

Teleutospores. Sori hypophyllous, on orbicular brown spots, minute, scattered or circinate, roundish, at first yellowish-brown, then brown; spores fusoid, generally rounded above and thickened (up to 5μ), hardly constricted, tapering below, smooth, yellowish or very pale brown, $28-52 \times 10-16\mu$, pedicels hyaline, persistent, as long as the spore or shorter.

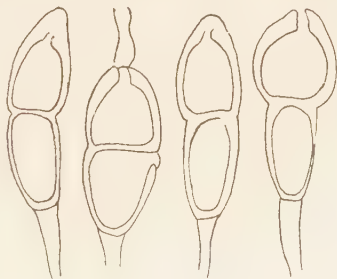


Fig. 119. *P. Veronicæ*.
Teleutospores.

On *Veronica montana*. June (or earlier) to October. Not common. (Fig. 119.)

Distinguished from *P. Veronicarum* by the very clear-coloured and narrower spores, which are less strongly thickened at the apex. It has also only one form of spore, viz. that with persistent pedicel which germinates as soon as mature. It does not occur on *V. alpina*.

DISTRIBUTION: Western and Central Europe.

42. **Puccinia Veronicarum** DC.

P. Veronicarum DC. Flor. fr. ii. 594. Cooke, Handb. p. 496; Micr.
Fung. p. 204. Plowr. Ured. p. 214. Sydow, Monog. i. 257.
Fischer, Ured. Schweiz, p. 323, f. 236. See Sacc. Syll. vii. 685.

Teleutospores. Sori hypophyllous, on irregular or roundish brown spots, circinate, minute, roundish, often confluent, some

compact, pulvinate and greyish, others brown and pulverulent :

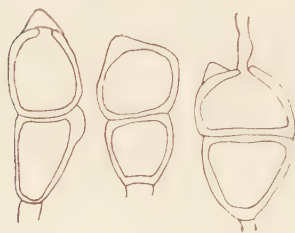


Fig. 120. *P. Veronicarum*. Teliospores on *V. alpina* (ex herb. Berkeley).

spores oblong or obovate, attenuated into a horny much thickened (up to 8μ) conical point at the apex, constricted, slightly tapering below, smooth, pale or dark chestnut-brown, $28-40 \times 14-19\mu$; pedicels hyaline or somewhat yellowish, rather long, deciduous or persistent.

On *Veronica alpina*, *V. officinalis* and perhaps other species. Not common. July - October. (Fig. 120.)

There are two forms of spores in this species; one, *fragilipes*, with deciduous pedicels; the other, *persistens*, with persistent pedicels. In the former, the sori are soon naked and pulverulent, the spore-wall is thicker and darker-coloured, and germination takes place only after a winter's rest. In the latter, the sori are compact, the spores are thin-walled and paler and germinate as soon as mature, upon the living plant. But occasionally both forms may be seen in the same sorus. It is the latter form that spreads the parasite during the summer; the former causes new infections in the following spring.

Distinguished from *P. Veronicæ* by the relatively broader spores, and the cone-shaped apical thickening. It is possible that the *Pucciniae* on other species of *Veronica*, included by the Sydows with this, are really distinct. But in Herb. Berkeley there is a *Puccinia* on *Veronica alpina*, from Ben Alder, Invernessshire (and also from Perthshire) which is undoubtedly this species. The sori are hypophyllous only, but cover the larger part of each leaf. The spores are quite smooth, by which it is distinguished from the continental form on *V. alpina*, which has the upper spore-cell occasionally warted on the upper part; this form (*P. albulensis* Magn.) has the sori densely gregarious on stems as well as leaves, sometimes covering a whole internode.

DISTRIBUTION: Europe generally.

43. *Puccinia Menthæ* Pers.

Aecidium Menthæ DC. Flor. fr. vi. 95. Cooke, Handb. p. 544; Micr. Fung. p. 199.

Trichobasis Labiatarum Lév.; Cooke, Micr. Fung. p. 224 p.p.

T. Clinopodii DC.; Cooke, Micr. Fung. p. 224 (?).

Puccinia Menthae Pers. Syn. p. 227. Cooke, Handb. p. 496; Micr. Fung. p. 204 p.p., pl. 4, f. 69, 70. Plowr. Ured. p. 157. Sacc. Syll. vii. 617. Sydow, Monogr. i. 282. Fischer, Ured. Schweiz, p. 168, f. 131. McAlpine, Rusts of Australia, p. 140, f. 250. *P. Clinopodii* DC.; Cooke, Micr. Fung. p. 205 (?).

Spermogones. Scattered or arranged in little groups, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous and often on the stems, arranged on the leaves in clusters on orange or purplish spots, or forming elongated patches on the stems and petioles which are much thickened and deformed, opening irregularly, margin scarcely torn, erect or even incurved; spores verruculose, pallid-yellow, $24-40 \times 17-28 \mu$.

Uredospores. Sori hypophyllous, on yellowish or brownish spots (or without spots), minute, roundish, scattered or aggregated, soon naked, surrounded by the ruptured epidermis, sometimes confluent, cinnamon; spores globose to obovate, echinulate, pallid-brown, $17-28 \times 14-19 \mu$, with three equatorial germ-pores.

Teleutospores. Sori similar, but dark-brown; spores subglobose to obovate, rounded at both ends, with a broad pale-coloured apical papilla, not or scarcely constricted, more or less indistinctly verruculose, sometimes smooth, dark-brown, $26-35 \times 19-23 \mu$; pedicels hyaline, slender, longer than the spore.



Fig. 121.
P. Menthae.
Teleutospore
on *M. aquatica*.

On *Mentha aquatica*, *M. arvensis*, *M. citrata*, *M. rotundifolia*, *M. silvestris*, *M. viridis*, *Origanum vulgare*, *Calamintha Clinopodium*, *C. officinalis*. May—October, teleutospores from August. Very common on garden Mint, rather common on some of the other species. (Fig. 121.)

There can be little doubt that this is a collective species. Points of difference are found in the finer or coarser warts of the teleutospores and in the length of the pedicel; but hitherto no certainty has been arrived at in delimiting the various forms. I have seen the warts quite distinctly on some of the teleutospores on *M. aquatica* and *M. arvensis*, when they are viewed dry, but other spores in the same sorus seemed perfectly smooth. The æcidium seems not to occur on all species, though it is common on

garden mint : perhaps those forms which are without it may hereafter be separated. But it has occurred on all the hosts mentioned above except *Origanum* and *M. rotundifolia* ; it may, however, according to Sydow, be merely facultative. The form on *C. Clinopodium* really shows less difference from that on *Mentha aquatica* than those on species of *Mentha* do from one another. But Cruchet was unable to infect any one of the four *M. arvensis*, *M. aquatica*, *M. silvestris*, *C. Clinopodium*, except by spores from the same species. As the result of his experiments, he divides *P. Menthae* into eight biological races, as it occurs on *Mentha* and *Calamintha* ; and the form on *Origanum* is also biologically distinct. The Australian form of *P. Menthae*, which is an introduced species on *M. Pulegium* and *M. laxiflora*, has no known æcidiospores, but occasional mesospores. Nothing seems to be known about the form on *Ajuga reptans* mentioned by Plowright, from Johnston's Flor. Berwick.

In garden mint (*M. viridis*) the mycelium of the æcidial stage is spread throughout the whole plant, even in the rhizome ; Klebahn was able to trace the hyphae in some cases nearly up to the growing point. It lasts for several years at least ; a bed of mint infested with it should be rooted up and burnt ; there is no cure for the disease, although I have found that cuttings taken from some of the more distant healthy-looking shoots and planted elsewhere grow up without the parasite. The mycelium of the two other stages is purely local. I have known the æcidia to occur for several years in a garden without being followed by uredo- or teleutospores so far as could be seen, and *vice-versâ*, in another case, these spores occurred but no æcidium was ever noticed.

DISTRIBUTION : Europe, Asia, Africa ; the American and Australian teleutospores are more strongly warted.

44. *Puccinia caulicola* Schneid.

Puccinia caulicola Schneid. in Jahresb. Schles. Gesell. 1870, p. 120.

Sydow, Monogr. i. 301. Fischer, Ured. Schweiz, p. 172, f. 133.

P. Schneideri Schröt. in Herb. Schles. Pilze, no. 448. Plowr. Ured. p. 201. Sacc. Syll. vii. 677.

Teleutospores. Sori on the stems and petioles, rarely on the leaves, scattered, occasionally confluent, minute, roundish or elongated, long covered by the bullate epidermis, at length pulverulent, black, then cinnamon-brown ; spores ellipsoid, rounded at both ends, apex sometimes thickened in a papilli-form fashion, rather constricted, smooth, pale-brown, 24—33 $\times$ 15—24 μ ; pedicels hyaline, thin, rather long, not very

deciduous; a few mesospores intermixed, each with a low broad pore-cap.

On *Thymus Serpyllum*. June—October. Very rare; links, Aberdeen (Prof. J. W. H. Trail). (Fig. 122.)

The presence of the mycelium causes the stems to stand more upright; the internodes are considerably lengthened, and the leaves fewer, so that the affected plants can be readily distinguished, as in *P. Betonicae*. The mycelium appears to be perennial, and the sori to be confined almost entirely to the stems, where they cause a slight thickening and are more frequent at the nodes than elsewhere.

DISTRIBUTION: Central and North-western Europe.

45. *Puccinia Glechomatis* DC.

P. Glechomatis DC. Encycl. viii. 245. Cooke, Handb. p. 496; Micr. Fung. p. 204, pl. 4, f. 73—4. Plowr. Ured. p. 214. Sacc. Syll. vii. 688. Sydow, Monogr. i. 277. Fischer, Ured. Schweiz, p. 327, f. 239.

Teleutospores. Sori hypophyllous or on the petioles, on brownish spots or sometimes none, $\frac{1}{2}$ —1 mm. diam., roundish, solitary and scattered, or more often subconfluent into rounded clusters as much as 4 mm. diam., on the stem and petioles often elongated, pulvinate, at first yellowish, then chestnut, and at last blackish; spores ellipsoid or oblong, with an acute or rounded horn-like process (8—12 μ high) which is often obliquely placed and falls off on germination, faintly constricted, rounded below, smooth, pale and clear-brown, 30—48 $\times$ 15—24 μ ; pedicels hyaline, persistent, as much as 75 μ long; an occasional mesospore is found.

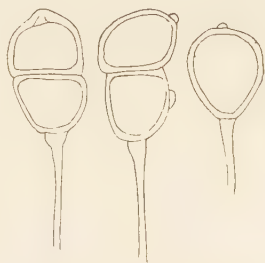


Fig. 122. *P. caulicola*.
Teleutospores and mesospore.

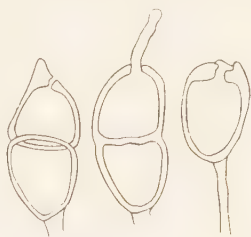


Fig. 123. *P. Glechomatis*.
Teleutospores and mesospore.

On leaves, petioles and stems of *Glechoma hederacea* (*Nepeta Glechoma*). June—October. Not uncommon. (Fig. 123.)

The sori are especially large, round and compact late in the season, when they produce spores which are darker and will not germinate immediately (as the others do), but only after the winter's rest. I have a specimen, resembling this species, on *Prunella vulgaris* from Sutton Park, Warwicks. ; Plowright mentions a similar one from Ben Lawers (*l.c.* p. 215).

DISTRIBUTION: Europe, Siberia, Japan.

46. *Puccinia Betonicæ* DC.

Puccinia Anemones var. *Betonicae* A. et S. Consp. p. 131.

P. Betonicae DC. Flor. fr. vi. 57. Cooke, Handb. p. 497; Micr. Fung. p. 205. Grove, in Gard. Chron. xxiv. 180, f. 38 (1885). Plowr. Ured. p. 199. Sacc. Syll. vii. 677 p.p. Sydow, Monogr. i. 275. Fischer, Ured. Schweiz, p. 173, f. 134.

Teleutospores. Sori hypophyllous, on pallid irregular spots, numerous, aggregated in patches, or more generally spreading over nearly the whole of a leaf, more or less crowded on the nerves, minute, perfectly round, surrounded by the torn erect epidermis, pulverulent, reddish-brown: spores ellipsoid to



Fig. 124. *P. Betonicæ*. Normal and abnormal teleutospores.

ovate, rounded above with a small paler hemispherical pore-cap, slightly constricted, rounded below, smooth, yellow-brown, $27-45 \times 15-24 \mu$; pedicels thin, hyaline, deciduous, about as long as the spore; a few oval mesospores intermixed.

On *Betonica officinalis* (*Stachys Betonica*). Not common. May—September. (Fig. 124.)

The affected leaves are paler, narrower, and stand more erect than the healthy ones. Besides the mesospores, other anomalies are occasionally

met with, viz. spores with three or more cells variously arranged. See Grove, Gardener's Chronicle, xxiv (1885), p. 180, f. 38. The mycelium is probably perennial.

DISTRIBUTION: Central and Western Europe.

47. *Puccinia annularis* Schlecht.

Uredo annularis Strauss in Wetter. Ann. ii. 106.

Puccinia annularis Schlecht. Flor. Berol. ii. 132 (1824). Plowr. Ured. p. 217. Sacc. Syll. vii. 689. Sydow, Monogr. i. 300. Fischer, Ured. Schweiz, p. 329, f. 240.

P. Scorodoniae Link. Spec. ii. 72 (1825). Cooke, Handb. p. 497; Micr. Fung. p. 205.

Teleutospores. Sori hypophyllous, on indefinite yellowish or brownish concave spots, at first minute, roundish, covered by the epidermis, in orbicular clusters, then naked, confluent, and forming a thick pulvinate mass, ferruginous-brown; spores oblong, rounded or attenuated at the apex and much thickened (up to 8μ), slightly constricted, rounded or attenuated at the base, smooth, very pale yellowish-brown, $30-54 \times 14-21\mu$; pedicels hyaline, persistent, as much as 80μ long.

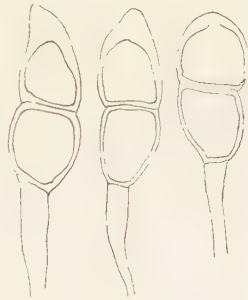


Fig. 125. *P. annularis*.
Teleutospores.

On *Teucrium Scorodonia*. July—October. Not common. (Fig. 125.)

Here, as in other Lepto-species, there seem to be two kinds of spores, those which germinate at once and those which will not germinate till the following year. The form on *T. Chamaedrys* (not yet found in Britain) has been proved to be biologically distinct.

DISTRIBUTION: Central and Southern Europe.

48. *Puccinia Convolvuli* Cast.

Uredo Betae β . *Convolvuli* Pers. Syn. p. 221.

Puccinia Convolvuli Cast. Obs. i. 16. Plowr. Ured. p. 146. Sacc. Syll. vii. 610. Sydow, Monogr. i. 319. Fischer, Ured. Schweiz, p. 322, f. 234.

[*Acidiospores*. *Acidia* hypophyllous, on brownish or purplish spots, more or less circinate, often on the petioles and then in elongated patches, cup-shaped, minute, with broad recurved torn white margin; spores delicately verruculose, pallid-yellow, $17-28\ \mu$.]

Uredospores. Sori scattered or circinate, minute, often confluent, soon naked, brown; spores more or less ellipsoid, rarely ovate, faintly echinulate, pale-brown, $22-30 \times 18-26\ \mu$, with two or three germ-pores just above the middle.



Fig. 126. *P. Convolvuli*.
Teleutospores on *Convolvulus sepium*, Poughkeepsie, U.S.A.

Teleutospores. Sori similar, but long covered by the grey epidermis, black-brown; spores ellipsoid to oblong, obtuse or rounded above, more or less thickened (up to $9\ \mu$), gently constricted, rounded below, smooth, chestnut-brown, $38-66 \times 18-30\ \mu$; with them are intermixed (according to Sydow) ovoid mesospores, much thickened at the apex, brown, $25-35 \times 20-26\ \mu$; pedicels brownish, thick, persistent, up to $35\ \mu$ long.

On *Convolvulus sepium* (Miss Jelly). June–October. Very rare. (Fig. 126.)

The connection of the acidiospores with the teleutospores was experimentally demonstrated by Arthur. According to Fischer, the uredospores often have a smooth median equatorial zone, of which I could see no trace. I have not seen the acidia.

DISTRIBUTION: Europe, Africa, Japan, North America.

49. *Puccinia Vincæ* Berk.

Uredo Vincæ DC. Flor. fr. vi. 70.

Trichobasis Vincæ Berk.; Cooke, Micr. Fung. p. 226, pl. 6, f. 130–1.

Puccinia Vincæ Berk. Engl. Fl. v. 364. Cooke, Handb. p. 497; Micr.

Fung. p. 205, pl. 6, f. 132. Plowr. Ured. p. 161, pl. 2, f. 11–14;

Gard. Chron. 1885, xxiv. 108, f. 22–3. Sacc. Syll. ix. 310.

Sydow, Monogr. i. 338. Fischer, Ured. Schweiz, p. 167, f. 130.

Spermogones. Hypophyllous or amphigenous, minute,

punctiform, brownish, often very numerous, scattered over the whole leaf-surface, sweet-scented, spherical, about $175\ \mu$ diam.

Uredospores. Sori hypophyllous, pallid-brown, of two kinds; *primary* irregular, often elongated and curved, crowded and confluent, naked; *secondary* scattered, on roundish dirty-brown spots, long covered by the epidermis; spores globose to pyriform, aculeate, pallid-brown, $20\text{--}32\ \mu$ diam. or $20\text{--}46 \times 16\text{--}24\ \mu$, with three germ-pores.

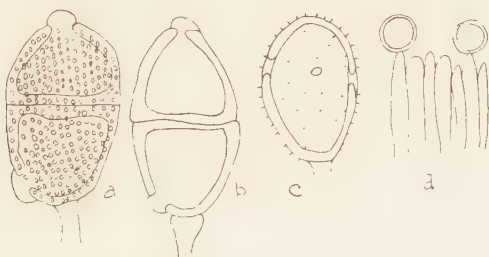


Fig. 127. *P. Vincæ*. a, teleutospore, seen dry; b, the same, seen wet; c, uredospore; d, the so-called æcidia. On *Vinca major*, all $\times 600$.

Teleutospores. Sori hypophyllous, on scarcely perceptible or conspicuous spots, minute, scattered or in groups, roundish or irregular, surrounded or half-covered by the torn epidermis, pulverulent, dark-brown: spores ellipsoid to oblong, rounded at both ends or attenuated downwards, hardly thickened at apex but with a pale papilla, not at all or faintly constricted, scrobiculate, ochreous-brown, $35\text{--}54 \times 18\text{--}27\ \mu$; epispore $3\text{--}4\ \mu$ thick; pedicels hyaline, deciduous, rather long.

On *Vinca major*, *V. minor*. Not common: Spermatogones in April; uredospores, May—June; teleutospores, July—October. (Fig. 127.)

This is one of the most remarkable species of *Puccinia* found in Britain. There is considerable difference of opinion about its structure. The bodies referred to in the description given by Plowright (*l.c.* p. 161) as “æcidia” are of a puzzling nature: they are not described by Sydow or Fischer, but are mistakenly considered by them as identical with the primary uredo-sori. They accompany the spermatogones on the under side of the leaves, and are flatly pulvinate subepidermal erumpent sori, surrounded by the erect

epidermis, and consisting of a floor of crowded erect narrow brownish hyphæ, each of which abstricts from its apex a small, smooth, round, thick-walled, nearly colourless spore, 8—10 μ diam. Plowright describes and figures these spores as forming basipetal chains, but this I could not see. The sori are numerous, about 1 mm. diam. and dark-brown with a greyish bloom, due apparently to the overlying spores. Can they be a parasitic fungus like *Darlucia Filum*, which has itself occasionally been considered as an additional spore-form of the Uredine on which it preyed?

The plants affected by the mycelium of the spermogones are permeated by it; they grow taller and more erect, the internodes are longer, the leaves paler, shorter, and thicker. Plowright considered this mycelium to be perennial, which is very probable. The spermogones have a distinct, but faint odour.

The sculpture of the teleutospores is very striking and almost unique. According to Sydow, it consists of a network of warts, but, in the British specimens which I have seen, it would be more correctly described as a series of pits arranged more or less in longitudinal lines (about 12 across the spore). Fischer represents the network as much finer. As is frequently the case, these markings can only be seen properly on the dry spore; they vanish almost completely when it is placed in water, unless it is emptied of its contents. The germ-pore of the lower cell is placed near the insertion of the pedicel, a very unusual position; it is covered with a pale papilla like the upper one.

DISTRIBUTION: Central and South-western Europe.

50. *Puccinia Gentianæ* Link.

Æcidium Gentianæ Jacz. Champ. Mont. p. 163 (1892), but ?

Uredo Gentianæ Strauss in Wetter, Annal. ii. 102 (1811).

Puccinia Gentianæ Link, Spec. ii. 73. W. G. Smith, Gard. Chron. xxiv. (1885) p. 372, f. 82. Cooke, Grevillea, xiv. 39. Plowr. Ured. p. 147. Sacc. Syll. vii. 604. Sydow, Monogr. i. 340. Fischer, Ured. Schweiz, p. 164, f. 126.

[*Spermogones*. Honey-coloured, in small clusters.

Æcidiospores. *Æcidia* hypophyllous or on the stems, on circular brown spots, in irregular clusters, cup-shaped, with torn white margin; spores delicately verruculose, orange, 16—23 $\times$ 14—17 μ .]

Uredospores. Sori amphigenous, but oftener on the upper surface, scattered or circinate, minute, roundish, at first covered by the epidermis, pale-chestnut; spores globose to ovoid,

aculeolate, brownish-yellow, $20-30 \times 18-24 \mu$, with two, rarely three, germ-pores.

Teleutospores. Sori similar and also on the stems, but pulverulent and black-brown; spores ellipsoid to ovoid, rounded at both ends, not thickened above, but sometimes with a low broad papilla, not constricted, smooth, dark-chestnut, $28-38 \times 24-30 \mu$; pedicels hyaline, thin, rather long, very deciduous; occasionally there are a few mesospores intermixed.

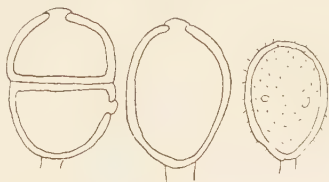


Fig. 128. *P. Gentianae*. Teleutospore, mesospore, and uredospore, on *G. acaulis*.

On *Gentiana acaulis*. Uredo- and teleutospores, Kew Gardens, August, 1905 (M. C. Cooke), and Horsham (W. G. Smith). (Fig. 128.)

I have a specimen on *G. Andrewsii*, from the United States, with exactly similar teleutospores. The æcidia are said to appear in April and June, and more frequently on the stems and peduncles than on the leaves. Jaczewski's *Æcidium* was on calyx, stem and leaf of *G. angustifolia*, on pale orange spots.

DISTRIBUTION : Europe, Siberia, East Indies, North America.

51. *Puccinia Primulæ* Duby.

Æcidium Primulæ DC. Flor. fr. vi. 90. Cooke, Handb. p. 544; Micr. Fung. p. 199.

Uredo Primulæ DC. Flor. fr. vi. 68.

Trichobasis Primulæ Cooke, Micr. Fung. p. 227.

Puccinia Primulæ Duby, Bot. Gall. ii. 891. Cooke, Handb. p. 495; Micr. Fung. p. 204. Plowr. Ured. p. 159. Sacc. Syll. vii. 612. Sydow, Monogr. i. 348. Fischer, Ured. Schweiz, p. 161, f. 124.

Æcidiospores. Æcidia hypophyllous, on yellowish spots, densely but irregularly clustered in roundish groups, shortly cylindrical, with a broad much cut revolute white margin; spores verruculose, orange, $17-23 \times 12-18 \mu$.

Uredospores. Sori hypophyllous, minute, scattered or circinate, roundish, soon naked brown: spores subglobose to ovoid, echinulate, pallid-brown, $20-23 \times 16-19 \mu$, with three germ-pores.



Fig. 129. *P. Primulae*.
Teleutospores and mesospore.

Teleutospores. Sori similar, but long covered by the grey epidermis, often confluent, or standing in circles round the aecidia or uredo-sori. blackish-brown; spores ovoid or oblong,

rounded at both ends, hardly thickened above but with a broad colourless papilla on each germ-pore, gently constricted, smooth, pallid-brown, $22-30 \times 15-18 \mu$; pedicels hyaline, short, deciduous; an occasional mesospore was seen.

On *Primula acaulis* (*vulgaris*). Not common. Aecidia in May; teleutospores, June—October. (Fig. 129.)

All three spore-forms may be found on the same leaf. The teleutospores are rather irregular in shape; mesospores are not infrequent, and Fischer describes and figures three-celled spores. This parasite is recorded on the continent also on *Primula elatior* and *P. veris*.

DISTRIBUTION: Central Europe.

52. *Puccinia Soldanellæ* Fekl.

Aecidium Soldanellæ Hornsch. in Rab. Krypt. Fl. p. 18 (1844).
Cooke, Handb. p. 537; Micr. Fung. p. 195.

Uredo Soldanellæ DC. Flor. fr. vi. 85 (1815).

Puccinia Soldanellæ Fekl. Symb. Myc. Nacht. iii. 14. Plowr. Ured. p. 159. Sacc. Syll. vii. 618. Sydow, Monogr. i. 349. Fischer, Ured. Schweiz, p. 159, f. 123.

Spermogones. Hypophyllous, numerous, punctiform, spherical.

Aecidiospores. Aecidia hypophyllous, scattered uniformly over nearly the whole leaf-surface, shortly cylindrical or urceolate, with a white denticulate revolute margin: spores delicately verruculose, yellowish, $18-26 \mu$.

[*Uredospores.* Sori generally epiphyllous, without spots,

scattered or circinate, minute, surrounded by the torn epidermis, brown; spores globose to ellipsoid, echinulate, pale-brown, $20-32 \times 18-28 \mu$; episore thick ($2-3 \mu$), with three germ-pores.

Teleutospores. Sori similar, but black-brown; spores ellipsoid to ovate-oblong, with a broad paler apical papilla ($5-8 \mu$ high), gently constricted, usually rounded below, smooth, brown, $35-55 \times 20-34 \mu$; pedicels hyaline, deciduous, up to 50μ long.]

On *Soldanella alpina* (Botanic Garden, Glasgow). All three spore-forms are said to occur together on the same plant in July and August.

The æcidium stage is most common; its mycelium is perennial and diffused through the plant, and causes a conspicuous change in the leaves; they become smaller, paler, and longer-stalked. Only this stage seems to have been met with in Britain; no doubt on imported plants, as has happened with *P. Gentianae*, *P. Pazschkei*, etc. Description of the uredo- and teleuto-stages after Sydow.

DISTRIBUTION: Central Europe.

53. *Puccinia Hydrocotyles* Cooke.

Caeoma Hydrocotyles Link, Sp. Plant. ii. 22.

Trichobasis Hydrocotyles Cooke, Journ. Bot. ii. 344; Handb. p. 530; Micr. Fung. p. 225, pl. 8, f. 168—9.

Puccinia Hydrocotyles Cooke, Grevillea, ix. 14. Ph. et Pl. Grevillea, xiii. 53. Plowr. Ured. p. 195. Sacc. Syll. vii. 641. Sydow, Monogr. i. 388.

[*Æcidiospores.* *Æcidia* amphigenous, distributed pretty uniformly over the whole leaf, rarely single, cup-shaped, with a yellowish deeply cut revolute margin; spores punctate, pale-yellowish, $19-26 \mu$.]

Uredospores. Sori amphigenous, scattered, now and then confluent, often circinate round a central larger one, very minute, long covered by the epidermis, at length naked, pulverulent, cinnamon; spores subglobose or ellipsoid, echinulate, brownish, $24-34 \times 20-27 \mu$, with two conspicuous germ-pores.

Teleutospores. A very few are found in the uredo-sori, ellipsoid to oblong, rounded at both ends, hardly thickened above, gently constricted, smooth, brown, $30-44 \times 18-28 \mu$; pedicels hyaline, thin, deciduous.

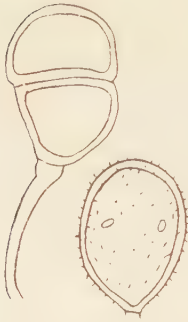


Fig. 130. *P. Hydrocotyles*.
Teleutospore and
uredospore.

On *Hydrocotyle vulgaris*. Rare: Kew Gardens; Epping Forest; Ireland, Co. Dublin. Uredospores, July—September; teleutospores, October. (Fig. 130.)

This species is very imperfectly known. The æcidium is recorded only from South America; in Europe the uredo-form alone has been observed, except for a few teleutospores in the uredo-sori. Lindroth describes the teleutospores (which are rare everywhere) as furnished with large isolated depressed and rounded warts, while those I have seen are perfectly smooth and with long and persistent pedicels. Cooke describes both uredo- and smooth teleutospores, intermixed, on *Hydrocotyle*, from Natal (*Grevillea l.c.*). Sydow states that the uredospores from all localities agree perfectly; those that I have examined from the Hawaiian Islands agree exactly with ours, having the same peculiar colour resembling a strong wash of “raw sienna.”

This species illustrates, in the Epping Forest locality, what can be frequently observed:—that, so long as the surroundings are undisturbed by man, many species of Fungi occur year after year continuously in the same spot. It is recorded as found there in 1863, 1864, 1871, 1882, and 1906, etc., and no doubt could have been found, or was found, there equally in all the intervening years.

DISTRIBUTION: France, Holland, Italy, North and South America, Natal, Pacific Islands.

54. *Puccinia Saniculæ* Grev.

Æcidium Saniculæ Carm. in Cooke's Brit. Æcid., Journ. Bot. ii. 39, pl. 14, f. 1. Cooke, Handb. p. 543; Micr. Fung. p. 198.

Puccinia Saniculæ Grev. Fl. Edin. p. 431. Cooke, Handb. p. 502; Micr. Fung. p. 208. Plowr. Ured. p. 160. Sacc. Syll. vii. 618. Sydow, Monogr. i. 413. Fischer, Ured. Schweiz, p. 122, f. 93.

Spermogones. Amphigenous, in little groups.

Æcidiospores. Æcidia hypophyllous or on the petioles, on

brown or purple spots, in small round clusters 2—4 mm. diam., elongated on the nerves and petioles, cup-shaped, with a whitish lobed revolute margin: spores tending to become ellipsoid, delicately verruculose, hyaline, $18-26 \times 15-22 \mu$.

Uredospores. Sori hypophyllous, on pale minute spots 2—3 mm. diam., scattered, rarely aggregated, minute, punctiform, pale-cinnamon; spore globose to ellipsoid, echinulate, not thickened above, brown, $25-38 \times 18-27 \mu$; epispore thick (up to $3\frac{1}{2} \mu$), with two (rarely three) germ-pores, with slightly swollen caps.

Teleutospores. Sori similar, but darker; spores ellipsoid or oblong, rounded at both ends, sometimes slightly thickened above and provided with a small papilla, hardly constricted, smooth, brown, $26-45 \times 18-26 \mu$; pedicels hyaline, thin, deciduous.

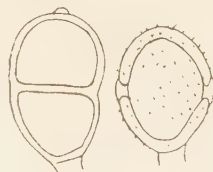


Fig. 131. *P. Saniculae*.
Teleutospore and uredospore.

On *Sanicula europaea*. Common. Æcidia, May and June; teleutospores, August—October; but I have found all three kinds of spores, in sheltered places, as early as April. (Fig. 131.)

DISTRIBUTION: Central and North-western Europe.

55. **Puccinia Cicutæ** Lasch.

Puccinia Cicutæ Lasch in Klotzsch, Herb. Myc. no. 787. Sydow, Monogr. i. 372.

Æcidiospores. Æcidia on the nerves of the leaves, on petioles and stems, in roundish or oblong groups as much as $1\frac{1}{2}$ cm. long, pustular, with a feebly developed peridium, golden-yellow; spores globose to ellipsoid, delicately punctate, subhyaline, $17-26 \times 10-20 \mu$.

Uredospores. Sori generally hypophyllous, scattered, minute, punctiform, pulverulent, cinnamon; spores subglobose to ovate, echinulate, yellow-brown, $18-28 \times 14-22 \mu$, with three germ-pores.

Teleutospores. Sori similar, but blackish-brown; spores ellipsoid or oblong, rounded at both ends or rarely attenuated downwards, not thickened above, gently constricted, somewhat

verruculose or distinctly verrucose-reticulated, even sometimes nearly smooth, brown, $28-46 \times 18-30 \mu$; pedicels hyaline, thin, short, deciduous.

On *Cicuta virosa*. Rare. Mentioned by Plowright in his arrangement of the British species, Trans. Brit. Myc. Soc. ii. 26; he assigns spermogones to it as well. I have seen no specimens.

The fungus is similar to *P. Smyrnii* in its æcidia and teleutospores, but differs in the presence of uredospores. Description after Sydow.

DISTRIBUTION: Central and Northern Europe, Siberia, Japan, North America.

56. *Puccinia Apii* Desm.

Trichobasis Apii Wallr.; Cooke, Micr. Fung. p. 224.

Puccinia Apii Desm. Cat. des Pl. omis. p. 25. Cooke, Handb. p. 502;

Micr. Fung. p. 208. Plowr. Ured. p. 156. Sydow, Monogr. i. 359.

Fischer, Ured. Schweiz, p. 119.

Spermogones. Hypophyllous, mostly surrounded by the æcidia, often circinate, shining reddish-brown.

Æcidiospores. Æcidia hypophyllous or on the petioles, on minute, irregular, conspicuous, yellowish spots, in roundish or on the petioles elongated clusters, shortly cylindrical, with white torn margin; spores delicately verruculose, orange, $17-24 \mu$.



Fig. 132. *P. Apii*. Telutospores and uredospore.

Uredospores. Sori hypophyllous, scattered, here and there confluent, surrounded by the epidermis, pulverulent, cinnamon-brown; spores ellipsoid to obovate or even subclavate, shortly echinulate, slightly thickened above ($3-5 \mu$), brownish-yellow, $24-35 \times 20-26 \mu$, with three equatorial germ-pores.

Teleutospores. Sori hypophyllous, rarely epiphyllous, if on

the petioles sometimes very large, scattered or confluent, roundish, pulverulent, blackish-brown: spores ellipsoid to oblong, rounded above, not thickened, hardly constricted, rounded or gently attenuated below, smooth, brown, $30-50 \times 15-23 \mu$; pedicels hyaline, thin, deciduous, about as long as the spore.

On *Apium graveolens*. Not common. *Æcidia* in May and June: teleutospores September—November. Distinguished from many of its close allies by the possession of an *æcidium*. (Fig. 132.)

DISTRIBUTION: Central and Northern Europe, East Indies. Japan, Tasmania.

57. *Puccinia Ægopodii* Mart.

Uredo Ægopodii Schum. Plant. Säll. ii. 233.

Puccinia Ægopodii Mart. Fl. Mosquen. p. 226. Cooke, Handb. p. 502; Micr. Fung. p. 208. Plowr. Ured. p. 201. Sacc. Syll. vii. 678 p.p. Sydow, Monogr. i. 353. Fischer, Ured. Schweiz, p. 105, f. 79.

Teleutospores. Sori amphigenous, but chiefly on the petioles and nerves, on thickened yellowish spots, small, but collected into dense irregular clusters and confluent, at first black, covered by the shining epidermis which splits in places longitudinally, soon naked, pulverulent, blackish-brown; spores oblong to ovoid, often irregularly angled and oblique, usually rounded above and with a pale wart-like apiculus $2-3 \mu$ high, hardly or not at all constricted (often broadest at the septum), more or less rounded below, smooth, clear chocolate-brown, granular, $28-48 \times 15-22 \mu$; pedicels hyaline, short, deciduous.



Fig. 133. *P. Ægopodii*. Teleutospores.

On *Ægopodium Podagraria*. April—August. Rather common. (Fig. 133.)

According to Tranzschel, a few isolated uredospores are to be found in the young sori; they are almost colourless, aculeate, $20-22 \times 18 \mu$. Semadeni proved that the spores of this fungus would infect only *Ægopodium*, and not any of the allied Umbellifers. In this species,

I find the septum of the teleutospores almost always comparatively broad and dark, far more so than in the majority of Puccinias.

DISTRIBUTION: Europe generally.

58. *Puccinia Bulbocastani* Fekl.

Æcidium Bulbocastani Cumino, Fung. Vall. Pis. 1804—5.

Æ. Bunii DC. Syn. p. 51. Cooke, Handb. p. 540 p.p.; Micr. Fung. p. 196. Plowr. Ured. p. 270 (?).

Puccinia Bulbocastani Fekl. Symb. Myc. p. 52. Cooke, Micr. Fung. p. 209. Sydow, Monogr. i. 363. Fischer, Ured. Schweiz, p. 133, f. 100.

Spermogones. Few, scattered amongst the æcidia, pale-yellowish.



Fig. 134. *P. Bulbocastani*. Whole plant of *C. Bulbocastanum*, with æcidia, nat. size. (Dunstable, April, 1896.)

Æcidiospores. Æcidia rarely on the leaves, hypophyllous, more often on the petioles and stems, densely crowded, causing considerable hypertrophy and curvature, between cup-shaped and pustulate, whitish, with a white irregularly torn margin; spores delicately verruculose, yellowish, $15-22\ \mu$.

Teleutospores. Sori amphigenous, scattered, minute, roundish, sometimes on the petioles confluent and elongated, long covered by the epidermis, black; spores ellipsoid to obovate-oblong, generally rounded at both ends, not thickened above, hardly constricted, minutely reticulate, brown, $25-42 \times 14-24\ \mu$; pedicels hyaline, thin, deciduous.

On *Curum* (*Bunium*) *Bulbocastanum*. Very rare. Dunstable (W. G. Smith). (Fig. 134.)

This species has no uredospores. Plowright confused together this and the *Puccinia tumida* on *Conopodium denudatum* (see his synonymy on pp. 206, 270). The latter species has no æcidia; this partly explains his remarks that he was unable to obtain any evidence of the connection between the æcidium and the Puccinia. Nevertheless, it appears not yet

to have been shown experimentally that the æcidia and the teleutospores described above are genetically connected. The markings on the teleutospore are really little, round, densely crowded pits, not actual reticulations as in *P. Chaerophylli*. — Plowright's statement (*l.c.* p. 270) that this æcidium was found by him on *Conopodium denudatum* is a mere slip of the memory, as I am informed by Mr W. G. Smith, in whose company it was found at Leagrave, near Dunstable, on the date mentioned.

DISTRIBUTION: Western and Central Europe, Algeria.

59. *Puccinia tumida* Grev.

Puccinia tumida Grev. Flor. Edin. p. 430 (1824). Sydow, Monogr. i. 376.

P. Bunii Winter; Plowr. Ured. p. 206.

P. Umbelliferarum DC.; Cooke, Micr. Fung. p. 208 p.p., pl. 4, f. 71—2.

Uredospores. Very few, oval, pale yellow, sparsely verrucose, $20-25 \times 15-18$, mingled with the teleutospores.

Teleutospores. Sori on the leaves, more often on the petioles and nerves, minute, but many crowded together and confluent in thickened elongated masses (up to 1 cm. long), covered by the ash-coloured epidermis, for a considerable time, black-brown; spores ellipsoid to ovate, rounded at both ends, not thickened above, hardly constricted, smooth, brownish, $26-36 \times 14-26 \mu$; pedicels hyaline, short, deciduous; an occasional mesospore is found.



Fig. 135. *P. tumida*. Teleutospore, mesospore and uredospore.

On *Carum majus* (= *Conopodium denudatum* = *Bunium flexuosum*). Not uncommon. April, May. (Fig. 135.)

Formerly confounded with *P. Bulbocastani*, from which it is distinguished by its very different habit. In that species the teleuto-sori are usually isolated on the leaves, and cause no swelling of the affected part as *P. tumida* always does: the latter moreover is without æcidia.

Plowright states that the mycelium is perennial, but this is doubtful. The sori appear to be confined to the radical leaves; I have never seen them on the cauline leaves or (what practically means the same thing, attacked plants do not flower. The fungus should therefore be looked for early, before the radical leaves begin to fade; the affected plants are then easily distinguished by their yellowish appearance.

The æcidium of *P. Conopodii-Bistortae* (q.v.) is sometimes to be found on the same plant as the teleuto-sori of *P. tumida*, though it is much rarer. Flowright mentions that, though the *Puccinia* is very common round King's Lynn, he could never find the æcidium which he at that time wrongly supposed to be connected with it. See also *Puccinia Bulbocastani*.

DISTRIBUTION: France, Germany, Norway.

60. *Puccinia Pimpinellæ* Mart.

Æcidium Pimpinellæ Kirchn. (1856); Cooke, Micr. Fung. p. 196.

Æ. Bunii DC.; Cooke, Handb. p. 540 p.p.

Uredo Pimpinellæ Strauss in Wetter, Annal. ii. 102 (1811).

Trichobasis Pimpinellæ Cooke, Micr. Fung. p. 224.

Puccinia Pimpinellæ Mart. Fl. Mosquen. ed. ii. p. 226. Cooke, Micr. Fung. p. 209. Plowr. Ured. p. 155 p.p. Sacc. Syll. vii. 616 p.p. Sydow, Monogr. i. 408. Fischer, Ured. Schweiz, p. 127, f. 97.

Spermogones. Amphigenous, mostly scattered amongst the æcidia, pale-yellowish.

Æcidiospores. *Æcidia* hypophyllous, in smaller or larger groups, often along the nerves and causing slight hypertrophy, between cup-shaped and pustulate, with a whitish irregularly cut margin; spores verruculose, subhyaline, 20—28 μ .

Uredospores. Sori hypophyllous, scattered, minute, pulverulent, cinnamon; spores globose to ellipsoid, echinulate, brown, 22—32 $\times$ 20—26 μ , with two (rarely three) germ-pores.

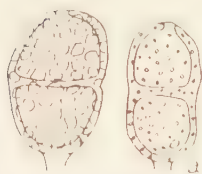


Fig. 136. *P. Pimpinellæ*.
Teleutospore, on *P. Saxifraga* (British); a, the same, on *P. magna* (after Fischer).

Teleutospores. Sori similar, but blackish-brown; spores ellipsoid, rounded at both ends, not thickened above, hardly constricted, reticulate, brown, 28—37 $\times$ 19—25 μ ; pedicels hyaline, deciduous, rather short.

On *Pimpinella magna*, *P. Saxifraga*. Not common. *Æcidia*, May and June; teleutospores, July—October. (Fig. 136.)

Very similar to *P. Chaerophylli*; distinguished from it especially by the uredospores, which have for the most part a thicker and darker membrane with only two germ-pores. The peridium of the æcidia is

better developed, and the teleutospores are plainly but not so densely reticulate. Klebahn proved by cultures that *P. Pimpinellae* is distinct from *P. Chaerophylli*, and Semadeni similarly proved its difference from that species and from *P. Heraclei*; the latter showed (Centralbl. f. Bakt. 2. xiii. 215) that it could be transferred to other species of the genus *Pimpinella*, but not to other genera of the Umbelliferae.

DISTRIBUTION: Europe, Asia Minor, East Indies, Algeria.

61. *Puccinia Bupleuri* Rud.

Æcidium Falcariae β. *Bupleuri-falcati* DC. Flor. fr. vi. 91.

Puccinia Bupleuri Rud. in Linnæa, iv. 514 (1829). Cooke, Grevillea, vi. 47. Plowr. Ured. p. 154.

P. Bupleuri-falcati Wint. Pilze, p. 212 (1884). Sydow, Monogr. i. 364. Fischer, Ured. Schweiz, p. 123, f. 94.

[*Spermogones*. Hypophyllous, numerous, generally scattered over the whole surface among the æcidia.

Æcidiospores. Æcidia hypophyllous, or a few epiphyllous, uniformly scattered, cup-shaped, with a torn white revolute margin; spores globose or ellipsoid, punctate, yellow, 16—24 μ .]

Uredospores. Sori amphigenous, scattered or occasionally circinate, on minute paler spots, small, rounded, cinnamon;

spores globose to ellipsoid, echinulate, yellow-brown, 19—24 $\times$ 17—22 μ , with three, four, or even five germ-pores.

Teleutospores. Sori amphigenous, minute, scattered, roundish, on the stems often larger and oblong, occasionally confluent, covered by the epidermis, at length naked, blackish-brown; spores oblong to clavate, rounded at both ends, not thickened above, hardly constricted, smooth, brown, 25—44 $\times$ 16—30 μ ; pedicels hyaline, thin, short, deciduous.

On *Bupleurum tenuissimum*. Very rare. Uredo- and teleutospores, Walton-on-the-Naze, August, 1887. (Fig. 137.)

The uredospores were found in small quantities among the teleutospores. Fischer says that the affected plants usually bear æcidia on every leaf, the leaves are narrower and paler, and the plants do not flower; the

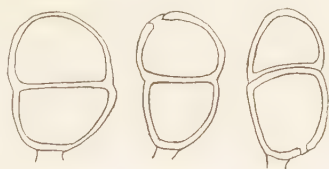


Fig. 137. *P. Bupleuri*. Teleutospores (Walton-on-the-Naze).

aecidium-stage appears in May and June, often abundantly. This applies especially to the parasite on *Bupleurum falcatum*, which is probably identical with that on *B. tenuissimum*, but the Walton plants bore flowers.

DISTRIBUTION: Europe, Asia Minor, East Indies, Yunnan.

62. *Puccinia Æthusæ* Mart.

Uredo Petroselini DC. Flor. fr. ii. 597.

Trichobasis Petroselini Berk. ; Cooke, Micr. Fung. p. 223 (?).

T. Cynapii DC. ; Cooke, Micr. Fung. p. 224.

Puccinia Æthusæ Mart. Flor. Mosq. ed. ii. p. 225 (1817). Cooke, Micr. Fung. p. 209.

P. bullata Wint. ; Plowr. Ured. p. 185 p.p.

P. Petroselini Lindr. Faun. et Flor. Fenn. xxii., no. 1, p. 84 (1902). Sydow, Monogr. i. 399, 889. Fischer, Ured. Schweiz, p. 112, f. 86.

Spermogones. Hypophyllous, yellow-brown, or almost hyaline.

Uredospores. Sori generally hypophyllous, scattered or in small clusters, very small, occasionally confluent and larger, pulverulent, cinnamon; spores globose to ellipsoid, echinulate either all over or only in the upper part, thickened above ($5-6\ \mu$), yellowish or brownish-yellow, $22-29 \times 21-25\ \mu$, with three (rarely two) equatorial germ-pores with conspicuous caps.

Teleutospores. Sori similar, but dark-brown, on the petioles and stems often larger, confluent and elongated; spores ellipsoid or ovate, rounded at both ends or slightly attenuated below, not thickened above, hardly constricted, smooth or nearly so, brown, $28-48 \times 18-25\ \mu$; pedicels hyaline, thin, short, deciduous.

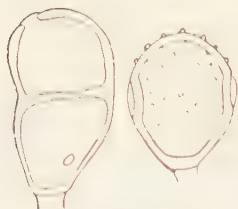


Fig. 138. *P. Æthusæ*.
Teleutospore and uredospore,
on *Æthusa*.

On *Æthusa Cynapium*, *Petroselinum sativum*. Not common. June—October. (Fig. 138.)

It is possible that the forms on these two hosts are distinct species, or at least biological races. Semadeni showed (Centralbl. f. Bakter. 2. xiii. 443) that, while he could infect several (non-British) species of Umbellifere with uredospores from *Æthusa Cynapium*, he could not infect *Petroselinum sativum*; at the same time he could find no morphological difference

between the two forms. *Conium maculatum* took the infection very weakly.

Lindroth and Fischer both describe the teleutopores as furnished with numerous minute embedded granules, otherwise even or with low rounded undulations, but Fischer figures them as perfectly smooth, as they certainly are in the cases I have seen. The uredospores are spiny in the upper part, nearly smooth below. When the few spines on the basal part are not to be discerned (as sometimes happens), they closely resemble those of *P. Conii*, except in being relatively broader; these two species are closely allied.

DISTRIBUTION: Central and Northern Europe.

63. *Puccinia Silai* Fckl.

Puccinia bullata Wint. Pilze, p. 191 p.p. Plowr. Ured. p. 183 p.p.

Sydow, Monogr. i. 403 p.p. Fischer, Ured. Schweiz, p. 119, f. 91 b.

P. Silai Fckl. Symb. Myc. p. 53. Cooke, Grevillea, xiv. 39.

Spermogones. Scattered, pale yellowish, accompanying the primary uredo-sori.

Uredospores. Primary sori generally on the nerves and petioles, elongated and confluent up to 3 cm. long, dark cinnamon; secondary hypophyllous or occasionally epiphyllous, scattered, minute, punctiform, brown; spores globose to ovate, more or less thickened above ($4-5\mu$), echinulate, brown, $25-40 \times 18-28\mu$, with three (rarely four) germ-pores.

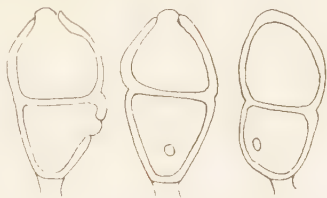


Fig. 139. *P. Silai*. Teleutospores.

Teleutospores. Sori minute, similar, but sometimes confluent on the stems, blackish; spores obovate or oblong, rounded at both ends or gently attenuated below, not thickened above, but often with a papilla, slightly constricted, smooth, brown, $28-42 \times 18-32\mu$; pedicels hyaline, rather short, deciduous.

On *Silvaus pratensis*. Rare; Pontrilas; Kew Gardens. August, September. (Fig. 139.)

This species was included by Sydow under the old *P. bullata* of Winter ; but since then it has been rendered probable by the experiments of Semadeni that it is distinct from most of the forms still remaining under that collective name (Centralbl. f. Bakter. 1904, 2. xiii. 530). Schröter proved that the spore-forms described above are genetically connected. The uredo- and teleutospores are generally found intermixed.

64. *Puccinia Angelicæ* Fekl.

Uredo Angelicæ Schum. Pl. Säll. ii. 233.

Trichobasis Angelicæ Cooke, Micr. Fung. p. 224.

Puccinia Angelicæ Fekl. Symb. Myc. p. 52. Cooke, Micr. Fung. p. 208. Sydow, Monogr. i. 356. Fischer, Ured. Schweiz, p. 117, f. 90.

P. Pimpinellæ Str. ; Plowr. Ured. p. 155 p.p.

Spermogones. Few, scattered, roundish, faintly coloured.

Uredospores. *Primary* sori chiefly along the nerves and petioles, or on the underside of the leaves in minute clusters on deep-yellow spots, at first deep-yellow, then darker, at length cinnamon; *secondary*, hypophyllous, occasionally epiphyllous, on minute paler spots, scattered, minute, pulverulent, yellow-cinnamon; spores obovate to oblong, echinulate, much thickened ($5-10\mu$) above, pale-brown, $25-40 \times 22-28\mu$, with three equatorial germ-pores.



Fig. 140. *P. Angelicæ*. Two normal teleutospores, also one abnormal and a mesospore; *a*, a uredospore; *b*, the primary uredo-sori (reduced). On *A. silvestris*.

Teleutospores. Sori amphigenous, scattered, minute, rounded, pulverulent, black-brown or black; spores oval to oblong, rounded and scarcely thickened above, hardly constricted, rounded or attenuated below, smooth, brown, $30-50 \times 16-24\mu$; pedicels hyaline, short, deciduous; an occasional mesospore is seen.

On *Angelica silvestris*. Not common. Uredospores, June and July; teleutospores, July—November. (Fig. 140.)

Distinguished especially by the very bright yellow primary uredo-sori, and by the slightly larger uredospores than in allied species. Semadeni proved that it would grow also on *Archangelica*, but not on *Æthusa Cynapium* or *Peucedanum palustre*. The primary uredo-sori should be compared with the æcidia of *P. Smyrni*. *P. Apii* is also closely allied, but differs in the possession of a true cup-shaped æcidium.

DISTRIBUTION: Central and Northern Europe, Turkestan.

65. *Puccinia bullata* Wint.

Uredo bullata Pers. Obs. Myc. i. 98 p.p.

P. bullata Wint. Pilze, p. 191 p.p. Sacc. Syll. vii. 634 p.p. Sydow,

Monogr. i. 403 p.p. Fischer, Ured. Schweiz, p. 119, f. 91 a.

P. Umbelliferarum and *P. bullaria*, p.p.

Spermogones. Pale yellowish.

Uredospores. Primary sori chiefly on the swollen nerves and petioles, elongated, as much as 3 cm. long, dark-cinnamon, secondary hypophyllous or rarely epiphyllous, scattered, minute, punctiform, brown; spores globose to obovate, echinulate, brown, apex more or less thickened, $25-40 \times 18-28 \mu$, with three or four germ-pores with swollen caps.

Teleutospores. Sori similar, often confluent on the stems, long covered by the epidermis, blackish-brown; spores

oblong to obovate, rounded above, scarcely thickened, hardly constricted, slightly narrowed below, smooth, uniformly brown, $30-45 \times 18-24 \mu$; pedicels hyaline, rather stout, deciduous.

On *Peucedanum palustre*. Shrapwick Bay, Somerset, 1883 (H. B. Waterfall). (Fig. 141.)

This species is placed temporarily in the collective group, *P. bullata* Wint. All the forms which were included under that head by Plowright are now separated on morphological or biological grounds, but nothing is known as yet about the *Puccinia* on *Peucedanum palustre*, from the latter point of view. It is a close ally of *P. Silai*.

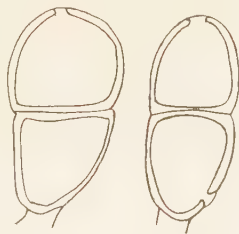


Fig. 141. *P. bullata*. Teleutospores on *Peucedanum palustre*, Shrapwick Bay.

66. **Puccinia Heraclei** Grev.

Trichobasis Heraclei Berk. ; Cooke, *Micr. Fung.* p. 225.

Puccinia Heraclei Grev. *Scot. Cr. Flor.* pl. 42. Cooke, *Handb.* p. 502 ; *Micr. Fung.* p. 208. Sydow, *Monogr.* i. 387. Fischer, *Ured. Schweiz*, p. 132.

P. Pimpinellae Strauss ; *Plowr. Ured.* p. 155 p.p.

Spermogones. Amphigenous, scattered amongst the aecidia, pale-yellowish.

Aecidiospores. Aecidia hypophyllous, frequently on the petioles and especially on the nerves of the leaves, on thickened yellowish spots, densely crowded in irregular clusters, often causing distortion, between cup-shaped and pustulate, sometimes almost spherical and superficial ; peridium feebly developed, opening by a rounded pore ; spores delicately verruculose, yellowish, $21-32 \times 18-28 \mu$.



Fig. 142. *P. Heraclei*. Aecidia on *Heracleum* (reduced).

Uredospores. Sori amphigenous, scattered, minute, chestnut-brown ; spores globose to ellipsoid, densely echinulate, pale-brown, $25-$

$32 \times 19-27 \mu$, with three or four germ-pores.

Teleutospores. Sori similar or more or less confluent on the nerves, surrounded by the ferruginous epidermis, pulverulent, blackish ; spores ellipsoid, rounded at both ends, hardly constricted, reticulated, brown, $26-37 \times 18-27 \mu$; pedicels hyaline, short, deciduous.

On *Heracleum Sphondylium*. Aecidia, March—June ; teleutospores, August. Not common. (Fig. 142.)

This species closely resembles *P. Chaerophylli*, but is distinguished by its less densely reticulated teleutospores. Semadeni proved by experiment that they are distinct species, but no one has as yet reared all the spore-forms of *P. Heraclei* from the basidiospores, as has been done for *P. Chaerophylli*. The aecidia of this species are more conspicuous than those of its allies ; they occur in swollen patches, reminding one of the aecidia on *Smyrniolum Olusatrum*, and being sometimes almost spherical and superficial might be compared to a group of miniature *Peziza vesiculosa*.

DISTRIBUTION : Central and North-western Europe.

67. **Puccinia Chaerophylli** Purt.

Puccinia Chaerophylli Purton, Midl. Flor. iii. 303. Sydow, Monogr. i. 367. Fischer, Ured. Schweiz, p. 129, f. 98.

P. Pimpinellae Str. ; Plowr. Ured. p. 155 p.p.

Spermogones. Pale-yellow, roundish.

Æcidiospores. *Æcidia* on the leaves and petioles, on the leaves scattered or circinate, on the petioles and nerves in dense elongated clusters and causing a slight hypertrophy, between cup-shaped and pustulate, yellowish; peridium poorly developed; spores verruculose, orange, $18-35 \times 16-26 \mu$.

Uredospores. Sori hypophyllous, scattered, minute, roundish, pulverulent, cinnamon: spores globose to obovate, echinulate, pale brownish-yellow, $20-30 \times 18-25 \mu$; with three usually equatorial germ-pores.

Teleutospores. Sori similar, but black-brown, on the petioles more elongated; spores ovate to oblong, rounded at both ends or gently attenuated below, not thickened above, slightly constricted, reticulated, yellowish-brown or brown, $24-36 \times 16-25 \mu$; pedicels hyaline, thin, as long as the spore or shorter.

On leaves, petioles, and stems of *Anthriscus silvestris*, *Chaerophyllum temulum*, *Myrrhis odorata*. Not common. *Æcidia*, May and June; teleutospores, July—October. (Fig. 143.)

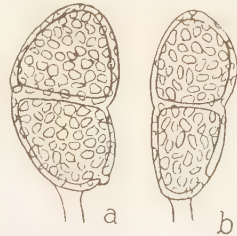


Fig. 143. *P. Chaerophylli*. Teleutospores, a, on *Anthriscus*, b, on *Myrrhis*.

It was proved experimentally by Klebahn that this parasite is not identical with *P. Pimpinellae*, and by Semadeni that it is not identical with that or with *P. Heraclei*. The latter also reared spermogones and *æcidia* from the basidiospores, and uredo- and teleutospores from the *æcidiospores*, of *P. Chaerophylli*; thus proving that all the spore-forms described above belong to the same species. The feeble development of the peridium and the pustule-like, not cup-shaped, *æcidia* are paralleled by those of *P. Heraclei*. The markings on the teleutospore are formed by a network of low ridges, with small polygonal or roundish meshes. The spore-reticulation is exactly of the same character as that of *P. Pimpinellae* except that the meshes are a little smaller and not quite so easily seen.

Semadeni showed that the spores from *A. silvestris* infected *M. odorata* readily (Centralbl. f. Bakt. pt. 2, xiii. 217—9), but whether the form on *C. temulum* belongs to the same species or is a biological race of it seems at present to be undetermined.

DISTRIBUTION: Central and Northern Europe, Siberia.

68. *Puccinia Conii* Fekl.

Uredo Conii Strauss in Wetter. Ann. ii. 96.

Trichobasis Conii Cooke, Micr. Fung. p. 225.

T. Umbellatarum Lév.; Cooke, Micr. Fung. p. 225 p.p.

Puccinia Conii Fekl. Symb. Myc. p. 53. Cooke, Handb. p. 209 p.p.

Sacc. Syll. xiv. 302. Sydow, Monogr. i. 375. Fischer, Ured.

Schweiz, p. 114, f. 87.

P. bullaria Link; Cooke, Handb. p. 503 p.p.

P. bullata Wint.; Plowr. Ured. p. 183 p.p.

Uredospores. Sori hypophyllous, occasionally on the petioles,

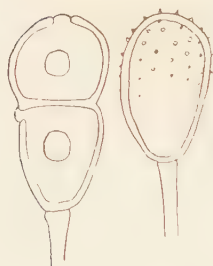


Fig. 144. *P. Conii*. Teleutospore and uredospore.

scattered, minute, rarely confluent, pulverulent, cinnamon; spores ellipsoid to obovate, thickened (up to 7μ) above and echinate in the upper part only, pale-brownish, $24-36 \times 17-26\mu$, with three germ-pores.

Teleutospores. Sori similar, but blackish-brown, on the stems and petioles often larger and long covered by the grey epidermis; spores ovate or ovate-oblong or even clavate, rounded at both

ends or attenuated below, not thickened at the apex but with a small papilla or pore-cap, hardly constricted, nearly or quite smooth, pale-brown, $30-48 \times 20-28\mu$; pedicels hyaline, short, deciduous.

On *Conium maculatum*. Not common; England, Wales, Ireland (Clare Island). August, September. (Fig. 144.)

Distinguished by the uredospores, which are echinate only in the upper half; the spines gradually diminish in size downwards and the lower half is quite smooth. The teleutospores which I have examined are quite smooth when empty, even under the highest power, but the protoplasm is very granular and presents a misleading effect at first sight.

69. **Puccinia Smyrnii** Corda.

Æcidium Bunii var. *Smyrnii-Olusatri* DC. Flor. fr. vi. 96.

Trichobasis Petroselinii Berk. ; Cooke, Handb. p. 529 p.p.

Puccinia Smyrnii Corda, Icon. iv. 18, f. 67 (1840). Cooke, Handb. p. 503 ; Micr. Fung. p. 209, pl. 3, f. 55—6. Plowr. Ured. p. 199. Sacc. Syll. vii. 670.

P. Smyrnii-Olusatri Lindr. Faun. et Flor. fenn. xxii. no. 1, p. 9 (1902). Sydow, Monogr. i. 416.

Spermogones. Epiphyllous, on sunken spots.

Æcidiospores. *Æcidia* hypophyllous or occasionally epiphyllous, in rather large irregular clusters, or on the petioles and stems in elongated groups, on yellow spots, hemispherical, yellow, opening by an irregular pore with a nearly entire margin; spores globose or ovate to fusiform or pyriform, delicately verruculose, yellowish, $16\text{--}40 \times 16\text{--}20 \mu$.

Teleutospores. Sori hypophyllous, on small yellow spots, scattered or a few together, minute, pulverulent, dark-brown; spores ellipsoid to oblong, rounded at both ends, not thickened above, hardly constricted, coarsely and remotely reticulate and tuberculate, brown, $30\text{--}48 \times 17\text{--}26 \mu$; pedicels hyaline, thin, deciduous, up to 60μ long; epispore rather thick.

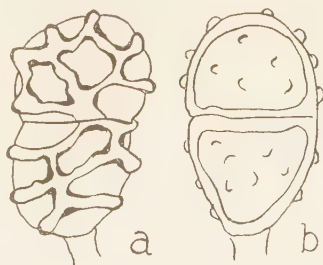


Fig. 145. *P. Smyrnii*. Teleutospores; a, as really sculptured; b, as seen when wet.

On *Smyrnium Olusatrum*.

Rather common near the coast.

Æcidia, April—June; teleutospores, June—August. (Fig. 145.)

The *æcidia* and teleuto-sori may occur on separate plants or on the same. The markings on the teleutospore form a wide-meshed network, which bears wart-like tubercles at the angles of the meshes. The *æcidiospores* bear more resemblance in form to uredospores than to what they really are; but they are produced in chains with intercalary cells in the usual way; they are not echinulate, but delicately verruculose; the markings can easily be seen on an empty spore. The peridium-cells are grossly verrucose on the inner surface, and are not arranged in regular rows. It is this irregularity which causes the peridium (as is usual in such cases) not to split into laciniae, but to open by a pore.

DISTRIBUTION: Central and Eastern Europe, Crete, Cyprus, Asia Minor, Algeria.

70. *Puccinia Circaeæ* Pers.

Puccinia Circaeæ Pers. Disp. Meth. p. 39, pl. 3, f. 4. Cooke, Handb. p. 507; Micr. Fung. p. 211. Plowr. Ured. p. 213. Sacc. Syll. vii. 686. Sydow, Monogr. i. 422. Fischer, Ured. Schweiz, p. 319, f. 232.



Fig. 146. *P. Circaeæ*.
Teleutospores.

Teleutospores. Sori hypophyllous, on sunken yellowish or purplish round spots, minute, pulvinate, brown, then with a greyish bloom, scattered or circinate and at length confluent in a thick crust: spores generally fusoid, rounded or conically attenuated above and much thickened (up to 12μ), gently constricted, attenuated downwards, smooth, yellowish-brown or brown, $25-40 \times 9-13\mu$; pedicels hyaline, persistent, about as long as the spore.

On *Circaea alpina*, *C. lutetiana*. Rather common. August—October. (Fig. 146.)

The sori of this species present two different forms: the first-formed are roundish, clear-brown, solitary or circinate and confluent; the later-formed, which appear round the others or on the stem and on the nerves of the leaves, are darker-brown and never greyish. All the spores are of the same shape, but the paler ones can germinate at once, in the sorus, while the darker ones rest until the following spring, as in *P. Veronicae*. There is another Uredine on the same host, even occurring on the same leaf: see *Pucciniastrum Circaeæ*.

DISTRIBUTION: Central and Northern Europe, North America, East Indies.

71. *Puccinia pulverulenta* Grev.

Aecidium Epilobii DC. Flor. fr. ii. 238. Cooke, Handb. p. 536; Micr. Fung. p. 195.

Uredo vagans var. *Epilobii-tetragoni* DC. Flor. fr. ii. 228.

Trichobasis Epilobii Berk.; Cooke, Micr. Fung. p. 226.

- Puccinia pulverulenta* Grev. Fl. Edin. p. 432 (1824). Cooke, Handb. p. 507; Micr. Fung. p. 211, pl. 4, f. 78—9. Plowr. Ured. p. 151.
P. Epilobii DC.; Sacc. Syll. vii. 608 p.p.
P. Epilobii-tetragoni Wint. Pilze, p. 214 (1884). Sydow, Monogr. i. 424. Fischer, Ured. Schweiz, p. 152, f. 118. McAlpine, Rusts of Australia, p. 170, f. 79—81.

Spermogones. Scattered among the æcidia, honey-coloured.

Æcidiospores. Æcidia hypophyllous or, when very abundant, also epiphyllous, scattered rather closely over nearly the whole surface of the leaf, cup-shaped, with a white torn revolute margin; spores very delicately verruculose, orange, 16—26 μ .

Uredospores. Sori hypophyllous, scattered or circinate, sometimes confluent, pulverulent, chestnut-brown; spores globose to ovoid, remotely echinulate, brown, 20—28 $\times$ 15—25 μ , with two germ-pores.

Teleutospores. Sori hypophyllous, often circinate, soon naked, pulverulent, dark-brown; spores ellipsoid or ovoid, rounded at both ends, somewhat thickened above (up to 5 μ) with a broad low cap-like addition, gently constricted, smooth, brownish, 24—35 $\times$ 14—20 μ ; pedicels hyaline, slender, deciduous.

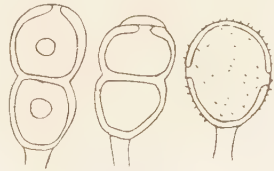


Fig. 147. *P. pulverulenta*. Teleutospores and uredospore.

On *Epilobium hirsutum*, *E. montanum*, *E. tetragonum*. Æcidia, May and June; teleutospores, June—November. Common. (Fig. 147.)

The æcidium-forming mycelium appears (but perhaps falsely) to be perennial, for the same plants are attacked year after year. The æcidia appear in May and cover leaf after leaf, as they are developed. The affected plants are easily recognisable by their much paler and yellowish colour. Soon the sori of uredo- and teleutospores begin to appear, at first on the same leaves, but afterwards on the later-formed leaves higher up the plant. In September and October the small last-formed leaves are thickly covered by the teleutospores; it is probably from the germination of these in spring that the next attack proceeds. The mycelium of the uredo- and teleuto-sori is strictly localised.

Plowright states (*loc.*) that the æcidiospores sown on young seedlings of *E. hirsutum* gave rise to æcidiospores in seventeen days, but very possibly

there is some oversight here, for Dietel obtained the *uredo* by sowing the æcidiospores from *E. tetragonum* on that plant; he also suggests that the form on *E. tetragonum* is biologically distinct from that on *E. hirsutum*, since on the latter he obtained no result.

DISTRIBUTION: Central and Northern Europe, Nova Zembla, Siberia, North America.

72. *Puccinia Epilobii* DC.

Puccinia Epilobii DC. Flor. fr. vi. 61. Cooke, Handb. p. 506; Micr. Fung. p. 211. Plowr. Ured. p. 202. Sydow, Monogr. i. 427. Fischer, Ured. Schweiz, p. 155, f. 120.

Teleutospores. Sori hypophyllous, scattered or rather crowded,

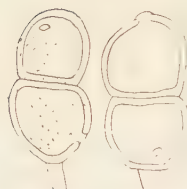


Fig. 148. *P. Epilobii*.
Teleutospores.

often uniformly distributed over the whole surface of the leaf, rarely confluent, surrounded by the torn epidermis, pulverulent, reddish-brown; spores ellipsoid, oblong or pyriform, rounded at both ends, hardly thickened above, but with a minute papilla, much constricted, minutely verruculose, clear brown, $27-48 \times 16-25 \mu$; pedicels hyaline, $10-16 \mu$ long.

On *Epilobium palustre*. Rare. May—August. A sub-alpine and arctic species. (Fig. 148.)

Distinguished from *P. pulverulenta* not only by its spores and the absence of the æcidium- and uredo-stages, but also by the smaller teleuto-sori which are scattered pretty uniformly over the leaf-surface. The mycelium seems to be perennial; it permeates the whole plant, and somewhat deforms the shoots, making the leaves smaller and thicker. The warts of the episporium are sometimes hardly perceptible, but can usually be seen if the spore is squeezed in the way recommended, see p. 83.

DISTRIBUTION: Central and Northern Europe.

73. *Puccinia Violæ* DC.

Æcidium Violæ Schum. Pl. Säml. ii. 224. Cooke, Handb. p. 543; Micr. Fung. p. 198.

Trichobasis Violarum Lév.; Cooke, Micr. Fung. p. 226.

- Puccinia Violae* DC. Flor. fr. vi. 62 (1815). Plowr. Ured. p. 152.
 Sydow, Monogr. i. 439. Sacc. Syll. vii. 609. Fischer, Ured.
 Schweiz, p. 139, f. 106.
P. Violarum Link, Sp. Plant. ii. 80 (1824). Cooke, Handb. p. 504 ;
 Micr. Fung. p. 210 ; Grevillea, iii. pl. 49, f. 5, 10 *a*, *b*.

Spermogones. Crowded in little clusters, yellowish.

Æcidiospores. *Æcidia* on all the green parts of the host, on the leaves often forming swollen yellowish spots, generally in roundish, or irregularly expanded, groups, on the stem sometimes scattered, flat, with a white irregularly torn revolute margin; spores delicately verruculose, orange, $16-24 \times 10-18 \mu$.



Fig. 149. *P. Violae*. *a*, leaf of *V. silvatica* with *æcidia*; *b*, teleutospore, seen wet; *c*, the same, seen dry; *d*, a mesospore.

Uredospores. Sori hypophyllous, scattered or circinate, minute, soon naked, pulverulent, cinnamon-brown; spores globose to ellipsoid, echinulate, brownish, $20-26 \times 17-23 \mu$, with two germ-pores.

Teleutospores. Sori similar, but darker; spores ellipsoid to oblong, rounded at both ends or gently attenuated below, thickened and paler above, hardly constricted, faintly punctate, chestnut-brown, $20-40 \times 15-23 \mu$; pedicels hyaline, deciduous, rather long; a few mesospores are found.

On all green parts of *Viola canina*, *V. hirta*, *V. odorata*, *V. Riviniana*, *V. silvestris*. Very common. *Æcidia*, April—June; teleutospores, August—November. (Fig. 149.)

The punctuation of the teleutospores is very delicate, like little pin-pricks, and can only be seen when they are dry; these spores are generally described as smooth and appear so except in the most favourable circumstances. The germ-pore of each of the cells is covered with a paler convex cap. The connection of all the spore-forms of this species was

experimentally proved by De Bary and Jacky. Bock (Centralbl. für Bakt. 2. xx. 586) showed that what appeared to be identical with *P. Violae* could also be artificially produced on *V. cornuta*, *V. lutea*, *V. tricolor*; the æcidia formed small or large crowded well-defined groups, and thereby differed from those of *P. aegra* which spread widely over the stems and leaves of their hosts, mostly standing alone and not collected in groups. In the latter, moreover, æcidia and teleutospores can be found in July at the same time (or even on the same leaf), which is not usually the case with *P. Violae*. This species can attack cultivated violets, but rarely does much harm; burning the infected plants is a sufficient remedy.

DISTRIBUTION: World-wide, except Australia.

74. *Puccinia aegra* Grove.

Æcidium depauperans Vize, Gard. Chron. (1876) pp. 175, 361, 437.

Cooke, Micr. Fung. p. 195; Grevillea, v. 57.

Puccinia aegra Grove, Journ. Bot. xxi. (1883) p. 274. Plowr. Ured. p. 158. Sacc. Syll. vii. 614.

P. depauperans Sydow, Monogr. i. 442 (1903).

Æcidiospores. Æcidia on all green parts of the host, particularly on the stems, not in clusters, but spread pretty uniformly over the whole surface, especially of the stems which are swollen and distorted, cup-shaped, with a white torn revolute margin; spores globose to ellipsoid, smooth, orange, $17-21 \times 14-16 \mu$.

Uredospores. Sori amphigenous, without spots, irregularly scattered or aggregated, occasionally confluent, long covered by the lead-coloured epidermis, cinnamon; spores globose to ellipsoid, delicately echinulate, brownish $20-28 \mu$ diam.



Fig. 150. *P. aegra*. Teleutospores and mesospore.

Teleutospores. Sori similar, but darker; spores ellipsoid or ovoid, rounded or gently attenuated above, where it is slightly thickened or rather surmounted by a minute subhyaline papilla, hardly constricted, usually rounded below, very delicately punctate or quite smooth, brown, $22-34 \times 16-20 \mu$; pedicels hyaline, short; a few mesospores are found.

On *Viola cornuta*, *V. lutea*, *V. tricolor*, and most of the many hybrid Violas and Pansies now cultivated in gardens. Fresh æidia are formed right through the summer till August, while those of *P. Violæ* cannot usually be found after early June. (Fig. 150.)

The mycelium of the æidia is perennial in the underground parts ; all the shoots which arise from the affected plant are deformed, the internodes are lengthened, the leaves become smaller, paler and often twisted. In *P. Violæ* this is not the case ; only a slight swelling arises at the part where the localised mycelium is producing its æidia. Bock (Centralbl. für Bakt. 2. xx. 586) found that he could produce the æidia of *P. Violæ* on the three species of *Viola* named above, by artificial infection ; but like others he still considered the two species as distinct on account of their different habit. Liro, on the contrary, considers them as the same. In my experience, the uredo- and teleuto-sori of *P. aegra* are larger, and remain longer covered by the epidermis, but the spores are identical.

This species can do considerable harm if allowed to spread ; there is no remedy, but all infected plants should be carefully uprooted and burnt. A *Viola*, badly attacked by the æidium, was once sent to the Gardener's Chronicle by a correspondent as "a hybrid between a fern and a violet."

DISTRIBUTION : Germany, Denmark.

75. ***Puccinia Fergussoni*** B. et Br.

Puccinia Fergussoni Berk. et Br. Ann. Nat. Hist. 1875, p. 35. Cooke, Grevillea, iii. 179, pl. 49, f. 10 c ; Micr. Fung. p. 210. Plowr. Ured. p. 207. Sacc. Syll. vii. 682. Sydow, Monogr. i. 444. Grove, Journ. Bot. 1912, p. 10.

Teleutospores. Sori hypophyllous or on the petioles, on large roundish or irregular yellow spots, in suborbicular or (on the petioles) elongated clusters up to $1\frac{1}{2}$ cm. long, densely crowded and confluent, long covered by the epidermis, then pulverulent, chocolate-brown ; spores irregular, generally oblong, attenuated or rarely rounded at both ends, thickened above in a conical form (up to 6μ), gently constricted, smooth, pale-brown, $26-45 \times 12-18\mu$; pedicels hyaline, thin, deciduous, up to 30μ long ; an occasional mesospore is found.

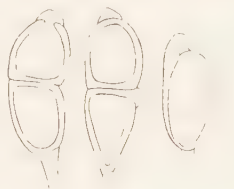


Fig. 151. *P. Fergussoni*.
Teleutospores and mesospore.

On *Viola palustris*. Rare; Wales, Scotland, and near Birmingham. The beginnings of the sori may be seen by the middle of May. (Fig. 151.)

This species is easily recognised by its large and pulvinate groups of sori. The mycelium spreads considerably beyond the part occupied by the spores, and consequently causes large yellow patches, usually only one or at most two on each leaf, each the result of a separate infection by the basidiospores.

P. asarina Cooke, Handbook, p. 504, Plowright, Uredineæ, p. 202 (*non* K. et S.), is this species, a mistake having been made in identifying the host-plant. In continental specimens of *P. asarina* Kunze, so far as I have seen, the sori on the lamina are as frequent on the upper leaf-surface as on the lower, whereas in *P. Fergussoni* they are entirely hypophyllous.

DISTRIBUTION: Northern Europe, North America (?).

76. *Puccinia argentata* Wint.

Æcidium argentatum Schultz, Prod. Flor. Starg. p. 454 (1806; teleutospores, on *Impatiens*).

Trichobasis Impatiensis Rab.; Cooke, Micr. Fung. p. 225.

Puccinia Noli-tangeris Corda, Icon. iv. 16, pl. 5, f. 57 (1840). Cooke, Handb. p. 504; Micr. Fung. p. 210.

P. argentata Winter, Pilze, p. 194 (1884). Plowr. Ured. p. 193. Sacc. Syll. vii. 639. Sydow, Monogr. i. 450. Fischer, Ured. Schweiz, p. 143, f. 109.

[*Spermogones*. Hypophyllous, scattered among the æcidia, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous, pretty uniformly distributed on discoloured swollen spots, on the petioles and stems more scattered, white, with a deeply-cut revolute margin; spores $18-22 \times 13-20 \mu$; contents golden-yellow.]

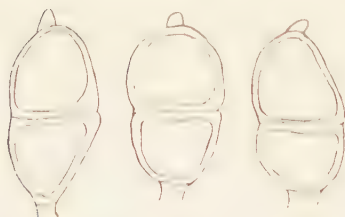


Fig. 152. *P. argentata*. Teleutospores, from the original specimen (L. Jenyns).

Uredospores. Sori hypophyllous, scattered or circinate, sometimes on minute yellowish spots, often confluent, covered by the silvery epidermis, then pulverulent, roundish, ochraceous; spores globose to broadly ellipsoid, delicately echinulate,

pale-yellowish. $16-22 \times 14-20 \mu$, with 3—5 (usually four) germ-pores.

Teleutospores. Sori similar, but chestnut-brown; spores ellipsoid to subclavate, with a colourless conical cap to each germ-pore, rounded or slightly attenuated at both ends, hardly constricted, smooth, pale-brownish, $25-38 \times 12-22 \mu$; pedicels hyaline, slender, short.

[*Æcidia* on *Adoxa Moschatellina*, April—June;] uredo and teleutospores on *Impatiens fulva*, *I. Noli-tangere*, May, August—October. Very rare; Albury, Surrey, October, 1864 (Rev. L. Jenyns), Guildford (Rev. W. A. Vize), Shere (M. C. Cooke), Kew Gardens (G. Masee). (Fig. 152.)

The teleutospores are at first produced in the same sori as the uredospores; the æcidial stage is not recorded, probably because it has been confounded with the æcidium of *P. albescens*, from which it is distinguished, according to Bubák, by its gold-coloured spores. I do not think this distinction will hold good; many of the specimens found in this country, which appear to be *P. albescens*, have golden-yellow spores. See under that species (p. 163).

The description given above of the spermogones and æcidia is taken from Bubák, who showed (Centralbl. für Bakt. 2. xii. 413) that they could produce the other stages on *Impatiens* in about ten days. He also showed that the æcidium could be produced on the *Adoxa* by over-wintered teleutospores; the incubation period was as long as one month, probably because the mycelium first permeated the whole plant, from the leaf to the stem, before producing spores. Afterwards he proved, contrary to his former opinion, that the mycelium does not perennate in the rhizome, but fresh infection must take place each spring (*ibid.* xvi. 150).

DISTRIBUTION: Central and Northern Europe, North America, Japan.

77. *Puccinia Buxi* DC.

Puccinia Buxi DC. Flor. fr. vi. 60. Cooke, Handb. p. 508; Mier. Fung. p. 212. Plowr. Ured. p. 217. Sacc. Syll. vii. 688. Sydow, Monogr. i. 453. Fischer, Ured. Schweiz, p. 316, f. 228—30.

Teleutospores. Sori amphigenous, on indefinite spots, scattered or confluent, hemispherical, pulvinate, hard, compact, soon naked, dark chestnut-brown or purplish-brown; spores

oblong to clavate, rounded above and not thickened, evidently constricted, usually attenuated below, smooth, brown, $55-90 \times 20-35 \mu$ (or even 100μ long); pedicels hyaline, persistent, very long, (reaching 160μ).

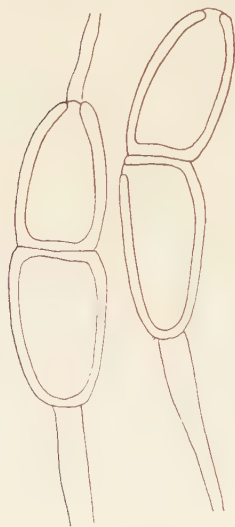


Fig. 153. *P. Buxi*.
Teleutospores.

On *Buxus sempervirens*. Rather common. September, October, lasting through the winter and following spring. (Fig. 153.)

The spores of this species easily fall apart into their component cells. Ed. Fischer proved that it has only the one spore-form: he gives (*l.c.*) figures showing the effect upon the leaf of an infection by the basidiospores. According to him, the teleutospores germinate in spring, and infect the delicate young leaves. The mycelium grows slowly. During the summer and autumn the infected spot becomes much thickened: the sori are produced in late autumn or during the following winter. This is exactly in accordance with the suggestion made by Plowright (*l.c.*), without any experimental evidence being at that time available.

DISTRIBUTION: Europe and Persia.

78. *Puccinia Malvacearum* Mont.

Puccinia Malvacearum Mont. in Gay, Hist. Chile, viii. 43. Cooke, Micr. Fung. p. 205; Grevillea, ii. 47, 137 and iii. pl. 35, pl. 49, f. 1. Plowr. Ured. p. 212. Sacc. Syll. vii. 686. Sydow, Monogr. i. 476. Fischer, Ured. Schweiz, p. 313, f. 227. McAlpine, Rusts of Australia, p. 178, f. 99, 100, 123-130, and pl. F, f. 28.

Teleutospores. Sori hypophyllous or amphigenous, and on the petioles and stems, on conspicuous yellow or orange spots, scattered but close together, small, hemispherical or on the stems elongated, pulvinate, compact, hard, at first pale-reddish, then reddish-brown; spores oblong to subfusoid, attenuated at both ends or rarely rounded above, thickened at the apex, gently constricted, smooth, yellowish-brown, $35-75 \times 12-26 \mu$; pedicels hyaline, persistent, short or as much as 150μ long; one-, three-, or even four-celled spores also occur.

On many species of Malvaceæ (of the subfamily Malveæ), especially on *Malva moschata*, *M. silvestris* and *Althaea rosea*. Very common. May—October (also in April and November). (Fig. 154.)

This is one of the most noticeable of the Uredinales. It is truly plurivorous; so far from being confined to a species, it is not even confined to a genus. In botanic gardens, where species of the family Malvaceæ are grown, side by side, in the same plot, the disease can be seen to spread to plants of all the allied genera—*Malva*, *Lavatera*, *Althaea*, *Kitaibelia*, *Malope*, *Abutilon*, *Sida*, *Sidalcea*, *Anoda*, *Malvastrum*, etc., have been recorded. A list containing many (nearly forty) species of these genera is given by Sydow, to which more are added by Fischer, McAlpine, and Dandeno. On all these it appears to be identical: artificial infections have proved that it can be transferred from *Malva* to *Althaea*, and *vice-versâ*.

It was first made known in 1852 by Montagne from a specimen found in Chili. It was observed in Australia in 1857 (McAlpine). In Europe it appeared in 1869, in South Africa in 1875, and it is now spread all over the world. It is believed that Chili was its native home; the rapidity of its distribution to other countries has few or no parallels among plant diseases.

It has been proved by many experimenters that it produces only the one kind of spore, which is capable of germinating at once when mature, though some can hibernate. It is a disputed point whether the mycelium can pass the winter in the plant or in the seed: the balance of evidence goes to show that fresh infections arise each year by the germination of over-wintered teleutospores, which can be found on all green parts, even on the fruits. See p. 48.

79. *Puccinia Pruni-spinosæ* Pers.

Æcidium punctatum Pers. in Uster. Annal. Botanik, xx. 135. Plowr. Ured. p. 268.

Æ. quadrifidum DC. Flor. fr. vi. 90. Cooke, Handb. p. 536; Micr. Fung. p. 194.

Puccinia Pruni-spinosæ Pers. Syn. p. 226 (1801). Sydow, Monogr. i. 484. Fischer, Ured. Schweiz, pp. 157, 547, ff. 21, 122, 340. McAlpine, Rusts of Australia, p. 171, f. 83—6 and pl. D, f. 19—20.

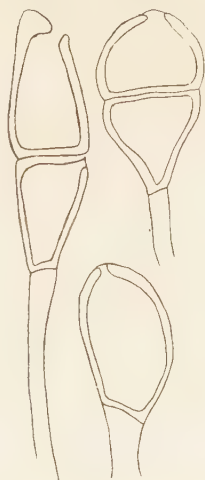


Fig. 154. *P. Malvacearum*.
Teleutospores and mesospore.

P. Pruni DC. Flor. fr. ii. 222 (1805). Plowr. Ured. p. 192. Sacc. Syll. vii. 648.

P. Prunorum Link, Sp. Pl. ii. 82 (1825). Cooke, Handb. p. 507; Micr. Fung. p. 211; Grevillea, iii. pl. 49, f. 11.

Tranzschelia punctata Arthur, North Americ. Fl. vii. 151.

Spermogones. Amphigenous, scattered, brown or blackish, very shallow, punctiform.

Æcidiospores. Æcidia hypophyllous, scattered over the



Fig. 155. *P. Pruni-spinosae*. Æcidia on *A. coronaria* (slightly reduced); *a*, an æcidium on *A. nemorosa*, Yorkshire, the normal form, and *b*, two less usual forms, $\times 30$.

whole surface, flat, with a broad revolute margin which is torn into few (3—5) lobes; spores roundish, pale yellowish-brown, finely verruculose, $16-24\ \mu$.

Uredospores. Sori hypophyllous, generally on minute coloured spots, scattered, but often crowded and confluent, soon naked, pulverulent, cinnamon-brown; spores ellip-

soid to fusiform, ovoid-oblong or sub-pyriform, smooth and more or less thickened at the summit in a conical shape and darker, paler and narrowed below, where they are sharply



Fig. 156. *P. Pruni-spinosae*. Two teliospores; *a*, lower half of a teliospore; *b*, uredospore; *c*, paraphysis; *d*, a cluster of teliospores. On Wild Plum. (All $\times 600$, except *d*, which is $\times 360$.)

verrucose or echinulate, pale-brown, $20-35 \times 10-18\ \mu$ (with three or four equatorial germ-pores, Arthur), mixed with yellowish-brown or pale capitate paraphyses more or less thickened at the apex.

Teleutospores. Sori similar but blackish-brown; spores ellipsoid to oblong, composed of two globose cells which readily separate (or lower cell often narrower, paler and imperfect), not thickened above, densely and coarsely verrucose, brown, $30 - 45 \times 18 - 25 \mu$; pedicels hyaline, very short, deciduous, springing in clusters of about 10—20 from a common base.

Æcidia on *Anemone coronaria*, *A. nemorosa*, April and May; uredo- and teleutospores on *Prunus domestica*, *P. insititia*, *P. spinosa*, also on cultivated species and varieties of *Prunus* and its allies, August—October. Common in certain districts. (Figs. 155, 156.)

The discovery of the heterecism of this parasite is comparatively recent. Tranzschel first showed (in 1904) that it was heteræcious, using *Anemone coronaria* and *Amygdalus communis* as the alternate hosts. F. T. Brooks, at Cambridge in 1911, laid fresh æcidiospores from the same species of *Anemone* on both sides of certain leaves of a "Victoria" Plum, leaving others uninoculated. The plant was enclosed by a bell-jar, and three weeks later twenty-three of the inoculated leaves were found to bear on their under-surface uredo-sori of *P. Pruni-spinosae*, while the control leaves showed no signs of the rust (New Phytologist, x. 207). Arthur, in the United States, proved a similar fact, but in that case the host of the alternate phase was *Hepatica acutiloba*, a very close ally of *Anemone*. The acidium is also reported on other species of *Hepatica*, *Anemone ranunculoides* and other species of *Anemone*, *Eranthis hiemalis*, and various species of *Thalictrum*.

Scribner (Report of the Dept. Agric. U.S.A. 1887) describes the *Puccinia* as found on Cherry, Apricot, and Peach: it is recorded by McAlpine on leaves, fruit and stems of Peach and Nectarine, and leaves and fruit of Almond and Apricot.

Trichobasis Rhamni of Cooke (Seem. Journ. Bot. ii. 344, iv. 104) on "*Rhamnus catharticus*," which was afterwards referred by him to this species (Handb. p. 508), is probably an error due to a mistake in the identification of the host. He states that the *Puccinia* on the same leaf was absolutely identical with *P. pruni-spinosae*, and omits the reference in the fourth edition of "Microscopic Fungi." No one else has found such a *Puccinia* on *Rhamnus*. The leaf in "Micr. Fung." ed. i. 210, is no doubt a *Prunus* leaf.

The mycelium of the æcidial stage is perennial; it penetrates in spring into the growing shoots which become deformed, the affected leaves are narrower and paler, and the flowers are usually imperfect or altogether wanting. These plants it is which cause fresh infections of the Plum-trees

every year; infection by over-wintered uredospores has been proved by Tranzschel to be possible, but as Brooks shows (*l. c.*) it is probably rare, because the plum-leaves are generally not affected until summer is well advanced. Fresh infections of the *Anemone* can, of course, be produced by the basidiospores of the over-wintered teleutospores.

The distinction usually made, by describing the uredospores as "echinulate," and the teleutospores as "verrucose," does not convey the exact truth; the markings on both are very similar, but the warts of the uredospores are sharp-pointed and usually turned downwards, while those of the teleutospores are often blunted, and always darker and more crowded.

The brothers Sydow describe a second form of uredospore, which I cannot find. The two cells of the teleutospore separate with the greatest readiness, and the lower cell which is very often paler and imperfect, could then be easily mistaken for a uredospore and has been so described and figured. The true uredospores, mentioned in the description, are very similar to amphispores, and have been mistaken at times for paraphyses. The teleutospores are attached by short fragile pedicels in bunches to a common basal cell. This is one of the characters of Arthur's genus, *Tranzschelia*.

Arthur describes (North Americ. Flora, p. 150) a second species of *Tranzschelia* (*P. cohaesa* Long, from Texas), agreeing in almost every minute detail with *P. Pruni-spinosae*, but having all its four spore-forms upon *Anemone decapetala*. In its teleutospores *P. fusca* (q.v.) agrees exactly with both of these, so that *P. cohaesa* may be regarded as a primitive form, from which both the others have been evolved. See Grove, New Phytologist, 1913, p. 89.

Jacky (Centralbl. f. Bakter. 2. viii. 658) divides *P. Pruni-spinosae* into two forms: *f. typica*, in which the teleutospore has both cells alike, on the three species of *Prunus* mentioned; and *f. discolor*, in which the teleutospore is thickened above, and the lower cell is paler, narrower and imperfect, on *Amygdalus communis* and *P. Persica*, less often on the other species. On *P. Armeniaca* both forms are found. This difference is by no means constant, however, and is hardly worthy of mention.

DISTRIBUTION: Europe, North and South America, Africa and Australia.

80. *Puccinia Rhodiolæ* B. et Br.

Puccinia Rhodiolæ B. et Br. Ann. Nat. Hist. ser. 2, v. 462. Cooke, Handb. p. 505; Mier. Fung. p. 211. Plowr. Ured. p. 207. Sacc. Syll. vii. 701. Sydow, Monogr. i. 491, f. 401.

Teleutospores. Sori amphigenous or on the stems, but generally hypophyllous, scattered or crowded and confluent, minute, roundish, surrounded by the torn epidermis, pulverulent, dark-brown; spores broadly ellipsoid, depressed, rounded at both ends, scarcely thickened above, not constricted, smooth, dark chestnut-brown, $20-35 \times 17-24 \mu$; pedicels hyaline, about as long as the spore: spores occasionally three-celled, like *Triphragmium*.

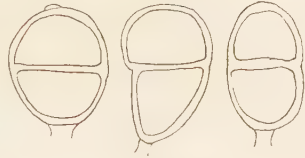


Fig. 157. *P. Rhodiolae*. Teleutospores, from Glen Callater (ex herb. Berkeley).

On *Sedum Rhodiola* (*roseum*). Very rare. Glen Callater, July, 1844 (W. Gardiner). (Fig. 157.)

DISTRIBUTION: Norway.

81. *Puccinia Umbilici* Guep.

Puccinia Umbilici Guep. in Duby, Bot. Gall. ii. 890. Cooke, Handb. p. 505; Micr. Fung. p. 211, pl. 4, f. 80—1. Plowr. Ured. p. 204. Sacc. Syll. vii. 700. Sydow, Monogr. i. 492, f. 403.

Teleutospores. Sori amphigenous or on the petioles, on yellowish spots, minute, roundish, usually circinate, at length confluent and forming large orbicular clusters up to 1 cm. diam., at first compact, then pulverulent, dark reddish-brown; spores broadly ellipsoid or subglobose, rounded at both ends, not thickened above but surmounted by a minute subhyaline apiculus or pore-cap, not constricted, smooth, bright chestnut-brown, $28-32 \times 18-26 \mu$, the cells often depressed (*i.e.* broader than long) and frequently oblique; pedicels short, hyaline.

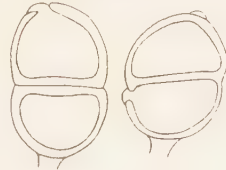


Fig. 158. *P. Umbilici*. Teleutospores.

On *Cotyledon Umbilicus*. Locally common. May and June; in mild localities it can be found even as early as January. (Fig. 158.)

DISTRIBUTION: France, Belgium, Portugal.

82. *Puccinia Ribis* DC.

Puccinia Ribis DC. Flor. fr. ii. 221. Gard. Chron. 1894, xvi. 135.
Trans. Brit. Myc. Soc. i. 57. Sacc. Syll. vii. 679. Sydow,
Monogr. i. 496.

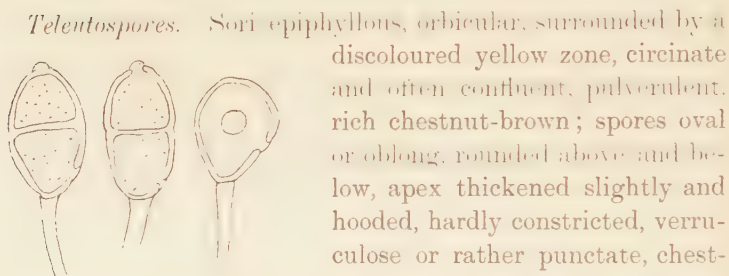


Fig. 159. *P. Ribis*. Teliospores and mesospore.

Teliospores. Sori epiphyllous, orbicular, surrounded by a discoloured yellow zone, circinate and often confluent, pulverulent, rich chestnut-brown; spores oval or oblong, rounded above and below, apex thickened slightly and hooded, hardly constricted, verruculose or rather punctate, chestnut-brown, $20-30 \times 15-20 \mu$; pedicels hyaline, thin, deciduous, about as long as the spore; a few

mesospores intermixed.

On leaves of *Ribes rubrum*. Very rare. Dallas Manse Garden, Elginshire, July 16, 1894 (Rev. Dr Keith). (Fig. 159.)

The pore of the lower cell is always towards the base, near the insertion of the pedicel. Eriksson showed that the teliospores do not germinate until they have passed through the winter. He considers the form on *Ribes rubrum* as biologically distinct from that on *R. nigrum* or *R. Grossularia*.

DISTRIBUTION: Central and Northern Europe, North America.

83. *Puccinia Saxifragæ* Schlecht.

Puccinia Saxifragæ Schlecht. Flor. Berol. ii. 134. Plowr. Ured. p. 208. Sacc. Syll. vii. 678. Sydow, Monogr. i. 500. Fischer, Ured. Schweiz, p. 151, f. 117.

P. Saxifragarum Cooke, Micr. Fung. p. 209 (*non* Handb. p. 506).

Teliospores. Sori generally hypophyllous, on discoloured spots, round, scattered or aggregated and confluent and then irregular, soon naked, pulverulent, dark-brown; spores ellipsoid or oblong, rounded at both ends or slightly attenuated below, slightly constricted, often surmounted by a rather large pale

conical papilla, marked with faint, sometimes curved, longitudinal striæ, pale-brown, $26-45 \times 14-20 \mu$; pedicels hyaline, slender, deciduous, not as long as the spore.

On leaves and petioles of *Saxifraga granulata*, *S. stellaris*, *S. umbrosa*. Rare. August. (Fig. 160.)

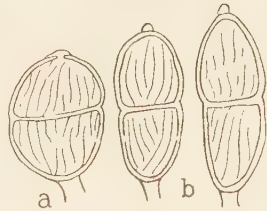


Fig. 160. *P. Saxifragae*. Teleutospores, *a*, on *S. umbrosa* (Ireland), *b*, on *S. stellaris* (Lochnagar).

The markings on the teleutospores are perfectly invisible when wet. This species has no connection with *Caeoma Saxifragae* which is also found on *S. granulata*. I have specimens from both Scotland and Ireland, the latter on *S. umbrosa* from Clare Island, and the former on *S. stellaris* from Lochnagar.

DISTRIBUTION: Central and Western Europe.

84. *Puccinia Pazschkei* Dietel.

Puccinia Pazschkei Diet. in Hedwig. 1891, p. 103; Ber. deutsch. Bot. Gesell. ix. 44, pl. 3, f. 15. Sacc. Syll. xi. 185. Sydow, Monogr. i. 503, f. 411. Fischer, Ured. Schweiz, p. 148, f. 113. Trans. Brit. Myc. Soc. iii. 123.

Teleutospores. Sori epiphyllous, about $\frac{1}{2}-1$ mm. wide, scattered or more often in orbicular groups 2—3 mm. diam., a few occasionally hypophyllous, surrounded by the swollen and torn epidermis, pulverulent, dark reddish-brown; spores ellipsoid or oblong, rounded at both ends, very slightly thickened above or with a minute flat papilla, gently constricted, faintly and irregularly verruculose, pale clear-brown, $25-35 \times 13-18 \mu$; pedicels hyaline, short, deciduous; a few mesospores intermixed.



Fig. 161. *P. Pazschkei*. Teleutospores and mesospore, (Sutton Coldfield).

On leaves of *Saxifraga longifolia*, Kew Gardens (G. Massee), Journ. Bot. xlv. 152. On a hybrid between *S. Cotyledon* and *S. aizoon*, Sutton Coldfield, April and May, 1911—12. (Fig. 161.)

A parasite doubtless introduced into this country with the plants. In the Sutton example, the sori form two or three perfectly round groups

towards the tip of each affected leaf, on the upper side. Fischer records it on *S. aizoon* and *S. elatior*.

DISTRIBUTION: Switzerland, Austria.

85. *Puccinia Chrysosplenii* Grev.

Puccinia Chrysosplenii Grev. in Engl. Flora, v. 367. Cooke, Handb. p. 506; Micr. Fung. p. 210. Plowr. Ured. p. 211. Sacc. Syll. vii. 685. Sydow, Monogr. i. 493. Fischer, Ured. Schweiz, p. 318, f. 231.

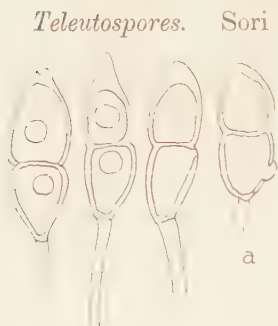


Fig. 162. *P. Chrysosplenii*. Teleutospores; a, the form *fragilipes*.

Teleutospores. Sori amphigenous, but generally hypophyllous, small, scattered or confluent, often circinate, roundish, pulvinate, pale-brown; spores of two kinds—(*forma persistens*) broadly fusoid, strongly thickened and more or less conical at the apex, rounded or slightly attenuated below, gently constricted, smooth, very pale-brown, $32-46 \times 10-15 \mu$; pedicels hyaline, rather long, persistent; (*forma fragilipes*) ob-

long-ellipsoid, with a conical papilla, distinctly constricted, yellowish-brown, with faint longitudinal ridges(?), $35-42 \times 14-19 \mu$; pedicels very deciduous.

On *Chrysosplenium alternifolium*, *C. oppositifolium*. Not common. End of March to August or September. (Fig. 162.)

The two kinds of spores are similar in form and function to those of *P. Veronicarum*; *forma persistens* consists of spores which germinate as soon as mature, *forma fragilipes* of spores which rest during the winter. It is said that the latter are scarce, but when present they form smaller sori which are less confluent, often solitary, and are frequently found on the upper leaf-surface. Compare the two similar kinds of spores in *P. Circueae*.

DISTRIBUTION: Central and Northern Europe, Eastern Asia.

86. *Puccinia Thalictri* Chev.

Puccinia Thalictri Chevallier, Flor. Paris, i. 417. Plowr. Ured. p. 206. Sacc. Syll. vii. 680. Sydow, Monogr. i. 550. Fischer, Ured. Schweiz, p. 94, f. 72.

Teleutospores. Sori hypophyllous, scattered or gregarious, often occupying the whole leaf, roundish, soon naked, pulverulent, dark-brown; spores much constricted, not thickened at the apex, the upper cell nearly globose, the lower globose, obovoid or clavate, generally narrower; the spores separate readily into their component cells, are covered with large pointed warts, dark-brown (the lower cell paler), $26-52 \times 18-30 \mu$; pedicels hyaline, deciduous.

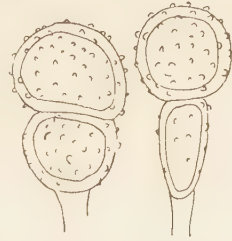


Fig. 163. *P. Thalictri*. Teleutospores, from Prof. Trail's specimens.

On *Thalictrum flavum*, *T. minus*. Very rare; Kinloch Rannoch, Perthshire (Prof. Trail); Kew Gardens. Autumn. (Fig. 163.)

This species has all the marks of a perennial mycelium. The same plants are attacked by it year after year; they are somewhat deformed and taller, with longer internodes, smaller and paler leaves and narrower segments. There is in Fischer a figure of a teleutospore with three cells, looking much like that of a *Phragmidium*. Cf. *Puccinia fusca*.

DISTRIBUTION: Northern and Central Europe, Siberia, North America.

87. *Puccinia fusca* Wint.

Æcidium fuscum Pers. in Linn. Syst. Veg. p. 1472 (teleutospores).

Puccinia Anemones Pers. Obs. ii. 24. Cooke, Handb. p. 503; Micr. Fung. p. 209, pl. 4, f. 65 -6.

P. fusca Wint. Pilze, p. 199. Plowr. Ured. p. 205. Sacc. Syll. vii. 669. Sydow, Monogr. i. 530. Fischer, Ured. Schweiz, p. 95, f. 73.

Spermogones. Hypophyllous, mixed with the teleuto-sori, blackish.

Teleutospores. Sori hypophyllous, rarely on the upper side, generally spread uniformly over the whole surface of the leaves, here and there confluent, small, round, pulverulent, dark-brown; spores very much constricted, composed of two almost globose or oblong cells which easily separate, densely

covered with large warts, brown, $30-55 \times 15-26$; pedicels hyaline, up to 40μ long; occasionally a few one- or three-celled spores are intermixed.

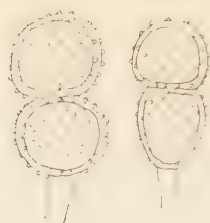


Fig. 164. *P. fusca*.
Teleutospores.

On *Anemone nemorosa*. Common.
March—June. (Fig. 164.)

It has been shown by De Bary and Ed. Fischer that the mycelium is perennial in the rhizome. The attacked plants are deformed and never flower; they bear paler and narrower leaves which are much thickened. The aecidia on the same host are not connected with this species (see *Ochropsora Sorbi* and *P. Pruni-spinosae*); in fact they do not appear until some time later than the teleutospores of *P. fusca* begin to show.

DISTRIBUTION: Europe, Siberia, North America.

88. *Puccinia Calthae* Link.

Aecidium Calthae Grev. Flor. Edin. p. 446. Cooke, Handb. p. 539; Micr. Fung. p. 196.

Puccinia Calthae Link, Sp. Plant. ii. 79. Cooke, Handb. p. 504; Micr. Fung. p. 210. Plowr. Ured. p. 145. Sacc. Syll. vii. 602. Sydow, Monogr. i. 540. Fischer, Ured. Schweiz, p. 310, f. 225.

Spermogones. In little clusters, honey-coloured.

Aecidiospores. Aecidia hypophyllous, in little clusters on roundish yellowish spots, or on the stems in elongated swellings, cup-shaped, with a torn whitish recurved margin; spores delicately verruculose, orange, $21-28 \mu$.

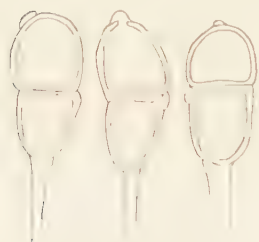


Fig. 165. *P. Calthae*.
Teleutospores.

Uredospores. Sori generally hypophyllous, minute, scattered, roundish, pulverulent, chestnut; spores globose to ellipsoid, echinulate, pale-chestnut, $22-30 \times 20-25 \mu$, with

two germ-pores in the upper half.

Teleutospores. Sori amphigenous, small, irregularly scattered or often circinate, pulverulent, but persistent, black-brown; spores oblong-clavate or fusoid, generally with a paler

conical papilla at the apex, hardly constricted, perfectly smooth, clear chestnut-brown, $30-44 \times 13-22 \mu$; pedicels hyaline, thick, persistent, up to 75μ long.

On *Caltha palustris*. Rather rare. *Æcidia*, May and June: teleutospores, July—October. (Fig. 165.)

There is another British species on *Caltha palustris*, *P. Zopfii*, which has been usually confounded with the present one in herbaria. It differs in having its teleutospores broader, darker, more oblong, and covered here and there with minute warts, but is otherwise similar in appearance. There are three others found on species of *Caltha* in North America, all so nearly allied that they are difficult of discrimination; but of these one has no uredospores, and the others have, so far as is known, teleutospores only. Some of these may be found in Britain.

DISTRIBUTION: Europe, Siberia, North America.

89. *Puccinia Zopfii* Winter.

Puccinia Zopfii Wint. in Hedw. 1880, p. 39, 107. Sydow, Monogr. i. 542. Fischer, Ured. Schweiz, p. 91, f. 70.

Spermogones. Amphigenous or on the petioles, in little clusters of 6—10, brownish when old.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, usually surrounding the groups of spermogones in scattered



Fig. 166. *P. Zopfii*. Leaf of *Caltha* with *æcidia*; two teleutospores.

roundish clusters 1—2 mm. diam. (elongated on the petioles), at first hemispherical, then shortly cup-shaped, flattish, yellow, with a short torn scarcely reflexed margin; spores delicately verruculose, yellow, $20-28 \mu$.

Uredospores. Sori generally hypophyllous, minute, scattered, punctiform, round, soon naked, surrounded by the erect epidermis, chestnut; spores ellipsoid, echinulate, brownish-yellow, $22-30 \times 20-25 \mu$, with two or three germ-pores.

Teleutospores. Sori similar, but darker; spores oblong to obovate, rounded at both ends, sometimes truncate above or slightly narrowed below, scarcely thickened but with a broad flat papilla at the apex, gently constricted, delicately verruculose, dark chestnut-brown, $35-60 \times 24-35 \mu$; pedicels nearly hyaline, short, deciduous.

On *Caltha palustris*. Rather rare; Shropshire, Scarborough, Rhydd-y-fen, Gullan Loch, Ireland (co. Dublin). *Æcidia* in May; teleutospores, August—December (June—September, Fischer). (Fig. 166.)

Distinguished from *P. Calthae* essentially by its teleutospores which are provided with a few, rather distant, minute warts, mostly towards the upper end; these are difficult to see except when viewed dry. The spores are also relatively much broader and not narrowed towards the summit, and are therefore easily seen to be distinct in shape; they are darker in colour and have shorter pedicels. The *æcidia* are not known to be different from those of *P. Calthae*; those described above probably belong to *P. Zopfi*, because they were found in the same neighbourhood as the teleutospores in Ireland: the cells of the peridium agreed with those figured by Fischer (*l.c.*). Krieg showed (Centralbl. f. Bakt. 2, xv. 259) that *P. Zopfi* is autoecious, like *P. Calthae*.

The two species have been frequently confounded in herbaria; but, if I may judge by the specimens I have seen, the teleuto-sori of *P. Calthae* are larger, more crowded, more often circinate, more compact, and remain longer covered by the epidermis than those of *P. Zopfi*, though this is not always so well marked.

DISTRIBUTION: Central Europe.

90. *Puccinia Lychnidearum* Link.

Puccinia Lychnidearum Link, Sp. Pl. ii. 80 (1825). Cooke, Handb. p. 505; Micr. Fung. p. 210 p.p. Plowr. Ured. p. 196.

P. Arenariae Winter, Pilze, p. 169 (1884). Plowr. Ured. p. 210. Sacc. Syll. vii. 683. Sydow, Monogr. i. 553. Fischer, Ured. Schweiz, p. 307, f. 224. McAlpine, Rusts of Australia, p. 177, f. 97 (introduced on *Stellaria media*).

P. Spergulae DC. ; Cooke, Micr. Fung. p. 210. Sydow, Monogr. i. 560.
P. Moehringiae Fekl. ; Cooke, Micr. Fung. p. 210.

Teleutospores. Sori hypophyllous or rarely on the stems, scattered or circinate, on pale spots, sometimes confluent, pulvinate, pallid-brown, then darker, greyish-pulverulent from the numerous basidiospores; spores oblong-fusoid or clavate,

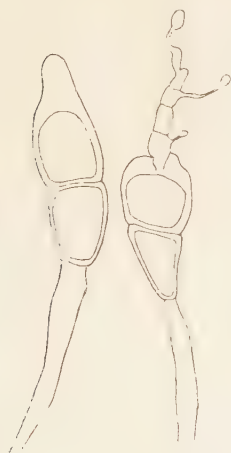


Fig. 167. *P. Lychnidearum*.
 Teleutospores, on *Lychnis diurna*.

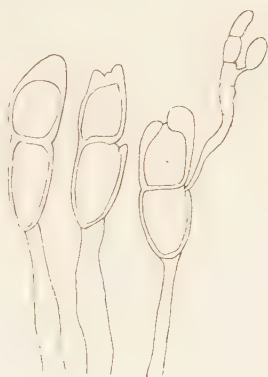


Fig. 168. *P. Lychnidearum*.
 Teleutospores, on *Arenaria trinervis*.

rounded or somewhat pointed above and more or less thickened (up to $10\ \mu$), gently constricted, rounded or attenuated below, smooth, yellowish-brown, $30-50 \times 10-20\ \mu$; pedicels hyaline, persistent, $60-85\ \mu$ long.

On various Caryophyllaceæ, such as *Dianthus barbatus*, *Lychnis diurna*, *L. vespertina*, *Arenaria trinervis*, *Gypsophila elegans*, *Sagina nodosa* (?), *Spergula arvensis* (?), *Stellaria Holostea*, *S. media*, *S. uliginosa*. May—November. It is most common on *Lychnis diurna*, on which as also on *Dianthus* the sori are remarkably circinate. (Figs. 167, 168.)

The two species, *P. Lychnidearum* and *P. Arenariae*, are united in Sydows' Monographia, on the ground that our present knowledge, derived from cultures, is insufficient to separate them, and that any apparent morphological distinctions break down completely when a long series of

specimens is examined. The spores are, however, variable in form and colour, and the sori differ in appearance and arrangement; no doubt the future will find this *Puccinia* divided into several biological races, if not into distinct species. Meanwhile, on morphological grounds alone, our British forms may be arranged under three heads:

1. forma *Lychnidearum* (Link), on *Lychnis*; sori medium-brown in colour, often greyish, remarkably circinate, on conspicuous yellow and purple spots.
2. forma *Dianthi* (DC.), on *Dianthus*; sori larger, darker, and more pulvinate, usually somewhat circinate; = *P. Dianthi* DC.
3. forma *Arenariae* (Schum.), on *Arenaria* and *Stellaria*; sori paler, not so circinate, spores paler; = *P. Moehringiae* Fekl.

The form on *Sagina procumbens* is so different that it is here reckoned as a separate species, *P. Saginae* K. et S. (q.v.). It will be noticed that Plowright separated *P. Lychnidearum* as a distinct species from *P. Arenariae*, chiefly on the ground that he considered the former to possess uredospores. It has been observed by all, however, that the common form on *Lychnis diurna* has no uredospores in its very abundant sori; it is therefore satisfactory to find that in Plowright's herbarium there are several leaves of *Lychnis diurna*, gathered by W. Phillips at Aberystwyth apparently on one occasion only (July 1873), on which are uredospores mixed with very few teleutospores. These he named *P. Lychnidearum*, but examination shows that they have no connection with the common fungus met with everywhere on the same host but belong to *P. Behenii* Othl. See under that species.

The *Puccinia* recorded by Plowright (*l.c.* p. 210) on *Spergula arvensis* may be a distinct species. See Cooke, *Micr. Fung.* p. 210. I have seen no specimens.

When mature, the cells of the teleutospores of *P. Lychnidearum* separate with great ease; they germinate readily while still in the sori, and the numerous basidiospores produced give them a greyish look, as happens also in other *Lepto*-species. I have specimens on *Arenaria trinervis* gathered in full germination at the end of May. During the process the spores become denticulate at the summit; in the case mentioned 75% of the spores were in this state. Such spores have sometimes been wrongly described as having digitate processes like those of *P. coronata*. — It was stated by De Bary that he had seen the germ-tubes of the basidiospores of *P. Dianthi* enter the host-plant through the stomata: no similar case has been detected by any other observer (see p. 38).

DISTRIBUTION: Europe, Siberia, East Indies, North and South America.

91. **P. Saginæ** K. et S.

Puccinia Saginæ K. et S. Exsicc. no. 221. Fuckel, Symb. Myc. p. 51.

P. Arenariæ Wint.; Plowr. Ured. p. 210 p.p. Sydow, Monogr. i. 553 p.p.

P. Lychnidearum Link; Cooke, Handb. p. 505; Micr. Fung. p. 210 p.p.

Teleutospores. Sori chiefly on the stems, compact, confluent, forming blackish-brown masses, about $\frac{1}{2}$ cm. long, encrusting at intervals the flowering stems which are slightly thickened at that spot, rarely on the leaves; spores oblong to oblong-clavate,

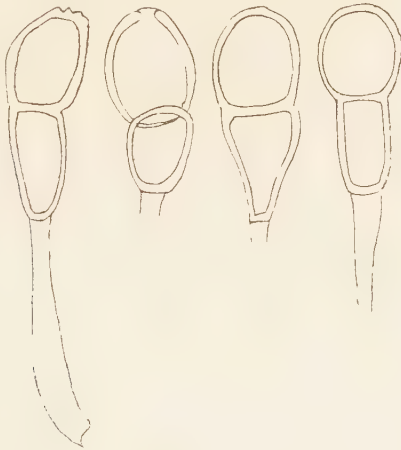


Fig. 169. *P. Saginæ*. Teleutospores, from the Ercal specimen.

rounded and not thickened above, slightly constricted, usually somewhat tapering below, smooth, very dilute brown, almost hyaline, $36-41 \times 15-19 \mu$; pedicels hyaline, rather stout, persistent, about as long as the spore.

On *Sagina procumbens*. Rare; specimen in Herb. Phillips (Brit. Mus.) from Ercal, near Wellington, under the name *Pucc. Lychnidearum*. (Fig. 169.)

The spores of this species, as well as the character of the sori, render it widely distinct from the various forms included under the name *P. Lychnidearum*; the most obvious difference is in the total want of thickening at the apex, unless this was due merely to the fact that all the spores had germinated, which did not seem to be the case.

92. **Puccinia Behenis** Otth.

Aecidium Behenis DC. Flor. fr. vi. 94 p.p.

Puccinia Behenis Otth, Mitth. Naturforsch. Gesell. Bern (1870), p. 89.

Fischer, Ured. Schweiz, p. 136, f. 103.

P. Silenes Schröt. in Winter, Pilze, p. 215 (1884). Cooke, Micr. Fung. p. 211. Plowr. Ured. p. 147. Sacc. Syll. vii. 605. Sydow, Monogr. i. 559.

Spermogones. In little clusters, honey-coloured.

Aecidiospores. Aecidia hypophyllous, on pallid-yellow spots,

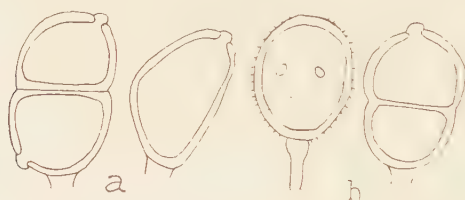


Fig. 170. *P. Behenis*. a, Teleutospore and mesospore, on *Silene inflata*; b, uredospore and teleutospore, on *Lychnis diurna*.

in orbicular clusters, minute, shortly cylindrical, with whitish torn margin; spores delicately verruculose, orange, $17-26 \times 14-20 \mu$, or 15μ diam.

Uredospores. Sori amphigenous, scattered or circinate, sometimes confluent, on paler spots, minute, cinnamon-brown; spores subglobose to ellipsoid, echinulate, pale-brown, $20-26 \times 17-22 \mu$, with three or four germ-pores.

Teleutospores. Sori similar, but black-brown; spores oblong to ellipsoid, rounded at both ends, faintly constricted, surmounted by a small pale apical papilla, smooth, chestnut-brown, $25-40 \times 16-26 \mu$; pedicels hyaline, short, deciduous.

On *Silene inflata* (= *S. latifolia*, *S. Cucubalus*) and *Lychnis diurna* (*dioica*). Not common. Uredo- and teleutospores, July—October. (Fig. 170.)

The description of the spermogones and aecidia is partly after Schröter, Sydow, and Fischer. The distinction of the aecidium of this species from that belonging to *Uromyces Behenis* is as follows:—The former has spermogones and uredospores, which accompany and follow it, but it is never accompanied by teleutospores. The early aecidia of the *Uromyces* are situated on purplish spots which show above, the later ones are usually

scattered singly: those of the *Puccinia* are in largish orbicular clusters and are rarely found singly; if not clustered, they spread over the whole leaf. In Plowright's herbarium are some leaves of *Lychnis diurna*, covered with uredo-sori, which he mistakenly assigned to *P. Lychnidearum*: there are no teleutospores of the latter, however, but a very few of *P. Behenii* were found in the same sori. See under *P. Lychnidearum*. The circinate arrangement of the sori, on paler spots, is very similar in both species.

DISTRIBUTION: Central and Western Europe.

93. *Puccinia Acetosæ* Körn.

Uredo Acetosæ Schum. Plant. Säll. ii. 231.

Puccinia Acetosæ Körn. in Hedwig. 1876, p. 184. Plowr. in Trans. Brit. Myc. Soc. i. 57. Sacc. Syll. vii. 638. Sydow, Monogr. i. 581. Fischer, Ured. Schweiz, p. 134, f. 101.

Uredospores. Sori amphigenous, scattered, minute, roundish on the leaves, elongated on the petioles and stems, soon naked, ferruginous-brown; spores globose to obovate, sparsely aculeate, brownish, $24-30 \times 20-23 \mu$, with two (rarely three) germ-pores.



Fig. 171. *P. Acetosæ*.
Teleutospores and uredospore.

Teleutospores. Sori similar, but dark-brown; spores ellipsoid, oblong, or subclavate, rounded at both ends or slightly attenuated below, not thickened at the apex, but furnished with a broad pore-cap, slightly constricted, delicately verruculose, chestnut-brown, $28-42 \times 19-24 \mu$; pedicels hyaline, slender, deciduous, as much as 35μ long.

On *Rumex Acetosa*. Malden, Yorkshire, July 16, 1894 (A. W. Saunders). Ireland, co. Antrim (J. Adams), August, 1909. Bewdley, Worcestershire, August, 1907, etc. (Fig. 171.)

There is no doubt that this species is often mistaken for *Uromyces Acetosæ*. In the absence of the two-celled teleutospores, which are rare, it could be distinguished mainly by its smaller sori, and more spiny uredospores (the spines are quite colourless). The teleutospores show the delicate warts more clearly on the upper cell; in the Bewdley specimens they were perceptible only with great care. Magnus proved that this species can pass the winter by its uredospores. It may be heteroecious.

DISTRIBUTION: Central and Northern Europe, Siberia, North America.

94. **Puccinia Oxyriæ** Fekl.

Puccinia Oxyriæ Fekl. Symb. Nacht. iii. 14. Cooke, Grevillea, xi. 15.
Plowr. Ured. p. 194. Sacc. Syll. vii. 642. Sydow, Monogr. i. 567.
Fischer, Ured. Schweiz, p. 135, f. 102.

Uredospores. Sori amphigenous, generally hypophyllous, on minute purplish spots, scattered or aggregated, rounded, sometimes confluent, surrounded by the cleft epidermis, cinnamon; spores globose to ovate, delicately echinulate, yellow-brown, $23-30 \times 20-26 \mu$.



Fig. 172. *P. Oxyriæ*. Teleutospores (from a Swiss specimen).

Teleutospores. Sori on the leaves similar, but also on the petioles and peduncles and then elongated, pulverulent, black-brown; spores oblong to obovate, rounded and slightly thickened or hooded above, constricted, generally rounded below, marked in the upper part with little unevennesses, almost as if corroded, brown, $30-46 \times 15-25 \mu$; pedicels nearly hyaline, deciduous, rather long.

On *Oxyria digyna* (*reniformis*). Rare; Skye (Buchanan White), Braemar (Prof. Trail). August. (Fig. 172.)

The teleutospores were described by the older authors as smooth; but, as Lagerheim first pointed out, they are really provided with faintly perceptible markings, especially visible towards the summit.

DISTRIBUTION: Switzerland, Norway, Iceland, Colorado.

95. **Puccinia Conopodii-Bistortæ** Kleb.

Puccinia Bistortæ DC. Flor. fr. vi. 61. Cooke, Micr. Fung. p. 204 ; Grevillea, ii. 161. Plowr. Ured. p. 192 (?). Sydow, Monogr. i. 571 (all *pro parte*). Soppitt, Grevillea, xxii. 45 ; Gard. Chron. 1895, xviii. 773.

P. Conopodii-Bistortæ Kleb. Wirtsw. Rostp. p. 318.

Æcidiospores. *Æcidia* on large swellings of a bright orange colour, immersed, spherical or flat, not at all cup-shaped, margin not projecting ; spores delicately verruculose, orange, 15—20 μ .

Uredospores. Sori hypophyllous, minute, roundish, yellowish-red, soon naked ; spores globose to shortly ellipsoid, finely echinulate, pale yellowish-brown, 21—24 μ .

Teleutospores. Sori hypophyllous, scattered or united in roundish groups, soon naked and pulverulent, dark-brown ; spores oblong or subclavate, rounded at both ends or slightly oblique at the apex, faintly constricted, clear yellowish-brown, 28—42 $\times$ 16—25 μ ; episore equally thick, smooth, but sometimes marked with a very few longitudinal or oblique rows of delicate warts ; no papilla on the germ-pores ; pedicels hyaline, short, very deciduous.



Fig. 173.
P. Conopodii-Bistortæ.
Teleutospore.

Æcidia on *Conopodium denudatum*, Yorkshire, May ; teleutospores on *Polygonum Bistorta*, June—August, not common. (Fig. 173.)

The Puccinias on *Pol. Bistorta* are not yet well known. There appear to be at least four (or five) distinct forms, which are divisible morphologically into two groups—(1) those whose teleutospores have no apical papilla, (2) those which have a small hemispherical papilla at the summit ; the latter are called by Sydow in the Monographia *P. mammillata* Schröt. (Pilz. Schles. p. 340). They are all heterœcious.

Of the former group, one form has an *æcidium* on *Conopodium*, and its other spore-stages on *P. Bistorta*. It is the one mentioned above ; the life-history was first demonstrated by Soppitt (*l. c.*). It is remarkable as being the *first* instance known of a heterœcious Puccinia that had its teleutospores on a Dicotyledon. The second form has its *æcidium* on *Angelica silvestris* and *Carum Carui* and its teleutospores on *Pol. Bistorta* and *Pol. viviparum*. It would perhaps be better divided into *P. Angelicæ-Bistortæ* Kleb. (= *P. Cari-Bistortæ*) and *P. Polygoni-vivipari* Karst. The connection in the former has been demonstrated by Klebahn and Fischer ;

as regards *Pol. viviparum* Klebahn expresses doubts, but Senadeni was able successfully to infect that species with uredospores from *Pol. Bistortae*. The form on *Pol. viviparum* is here kept provisionally distinct, since the æcidium on *Angelica* has not been found in Britain.

Of the second group, *P. mammillata*, there are two biological races—(1) *P. Mei-mammillata* Senadeni, on *Meum*, and (2) *P. Angelicae-mammillata* Klebahn, on *Angelica*. Neither of these has been found in Britain. All the four of these are closely allied; in Sydows' Monographia it is suggested that possibly in all these cases the æcidium on the Umbellifer is merely facultative and the Puccinia can maintain itself without that aid.

96. *Puccinia Polygoni-vivipari* Karst.

Puccinia Bistortae DC. ; Cooke, Grevillea, ii. 161 ; Mier. Fung. p. 204 p.p. Plowr. Ured. p. 192. Sacc. Syll. vii. 638. Sydow, Monogr. i. 571 p.p.

P. Polygoni-vivipari Karst. Enum. Fung. Lapp. p. 221. Fischer, Ured. Schweiz, p. 100, f. 76 (?).

Uredospores. Sori hypophyllous, scattered, small, roundish, cinnamon-brown, girt by the erect epidermis; spores roundish to ellipsoid, finely echinulate, pale-brown, $20-23 \times 16-17 \mu$.

Teleutospores. Sori similar, but blackish-brown; spores elliptical to obovate-oblong, rounded and not thickened above,



Fig. 174. *P. Polygoni-vivipari*. a, two teleutospores from Mar Lodge; b, uredo- and teleutospore from a specimen issued by Fuckel, Symb. Myc. 57; both on *Polygonum viviparum*.

hardly or not at all constricted, rounded or slightly tapering below, smooth, brown, $20-30 \times 15-20 \mu$; epispore very thin and translucent; no papilla on the germ-pores; pedicels deciduous, short.

On *Polygonum viviparum*. Very rare. Near Mar Lodge, August, 1822 (Dr Greville). Braemar, August, 1882 (Prof. Trail). (Fig. 174.)

This species is closely allied to *P. Conopodii-Bistortae* (q. v.), but in the absence of all biological information is best kept distinct. I have

seen no British specimens but those collected at Mar Lodge and Braemar, which are described above; the spores of these agree with those of a specimen on *Pol. viviparum* issued by Fuckel (see Symb. Myc. p. 57). It is a purely Alpine species.

97. *Puccinia Polygoni-amphibii* Pers.

Æcidium Geranii DC. ; Cooke, Handb. p. 543 ; Micr. Fung. p. 199 p.p.(?).

Æ. sanguinolentum Lindr. Myk. Notiz. in Bot. Notis. 1900, p. 241.

Uredo Polygonorum DC. ; Grev. Sc. Cr. Fl. pl. 80.

Trichobasis Polygonorum Berk. ; Cooke, Micr. Fung. p. 226 p.p.

Puccinia Polygonorum Link ; Cooke, Handb. p. 495 ; Micr. Fung. p. 203 p.p.

P. Polygoni Pers. ; Plowr. Ured. p. 188 p.p. Sacc. Syll. vii. 636 p.p.

P. Polygoni-amphibii Pers. Syn. p. 227 ; Sydow, Monogr. i. 569 p.p. Fischer, Ured. Schweiz, p. 301, f. 220.

[*Spermogones*. Few, amphigenous.

Æcidiospores. *Æcidia* hypophyllous, mostly in concentric groups, on well-marked spots which are deep-red or purplish and often surrounded by a conspicuous greenish-yellow zone, sometimes occupying the greater part of a leaf, cup-shaped, with a much cut recurved margin; spores finely punctate-verruculose, yellowish, 18—28 μ .]

Uredospores. Sori amphigenous, more often hypophyllous, scattered, roundish, soon naked, pulverulent, brownish; spores ellipsoid to obovate, faintly echinulate, yellowish-brown, 25—28 $\times$ 18—21 μ , with two germ-pores in the upper half.

Teleutospores. Sori chiefly hypophyllous, not projecting, long covered by the epidermis, surrounding the uredo-sori in a circular fashion, dark-brown; spores oblong to clavate, rounded and thickened above (5—12 μ), often obliquely conical at the apex, more or less tapering below, gently constricted, smooth, yellow-brown, 35—52 $\times$ 16—22 μ ; pedicels nearly hyaline, persistent.

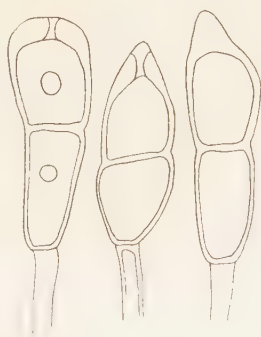


Fig. 175. *P. Polygoni-amphibii*. Teleutospores, on *P. amphibium*.

[*Æcidia* on *Geranium pratense*, *G. silvaticum*:] uredo- and telentosporos on *Polygonum amphibium*, *P. lapathifolium*, July – October; not uncommon. Klebahn and Bubák report the *æcidium* on *G. molle*, *G. phaeum* and other species. (Fig. 175.)

Teleutospores are found not only in the separate sori described above, but also in the old uredo-sori. These latter spores are rounded at the apex; those which grow in distinct sori often have the thickening cap forced to one side, presumably by the pressure of the persistent epidermis. For the distinctions of the *æcidium* of this *Puccinia* from that of *Uromyces Geranii* which grows upon the same hosts, see under that species (p. 104).

The proof of the connection of the *æcidium* with the *Puccinia* was first given by Tranzschel in Russia, and has since been confirmed by Bubák. I have not seen any British specimens of *Æcidium sanguinolentum*; the description given above is taken from Lindroth. Similarly in Switzerland, Fischer records only the uredo- and telentosporos. On *Polygonum amphibium* they seem to be confined to the terrestrial form: I have never seen them on the floating leaves.

DISTRIBUTION: World-wide.

98. *Puccinia Polygoni-Convulvuli* DC.

Puccinia Polygoni-amphibii Pers.; Sydow, Monogr. i. 569 p.p.

P. Polygoni-Convulvuli DC. Flor. fr. vi. 61.

P. Polygoni Plowr. Ured. p. 188 p.p. Sacc. Syll. vii. 636 p.p.

Fischer, Ured. Schweiz, p. 303, f. 221.

Spermogones and *Æcidia*. Presumably similar to those of the preceding species.

Uredospores. Sori hypophyllous, roundish, soon naked, brown; spores ellipsoid to obovate, echinulate, clear yellowish-brown, $24-30 \times 15-20 \mu$, with two opposite germ-pores.

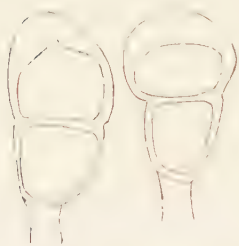


Fig. 176. *P. Polygoni-Convulvuli*. Teleutospores (ex herb. Cooke).

Teleutospores. Sori hypophyllous, scattered, roundish, compact, pulvinate, about $\frac{1}{2}$ mm. diam., soon naked and pulverulent, black; spores oblong to clavate, rounded or occasionally conical above and thickened (up to 8μ), faintly constricted, gently attenuated below, smooth, brown, $32-45 \times 18-21 \mu$; pedicels clear yellow-brown, persistent, nearly as long as the spore.

Æcidia on *Geranium pusillum*, and possibly also on *G. molle*, *G. rotundifolium*: uredo- and telentospores on *Polygonum Convolvulus*, August and September. Uncommon. (Fig. 176.)

The connection of the *æcidium* on the first-named host and the *Puccinia* on *Pol. Convolvulus* has been experimentally demonstrated by Tranzschel. It is possible that the same parasite also attacks *P. dumetorum*, *P. Persicaria* and others. The *æcidium* is not known for certain to have occurred in Britain. The teleuto-sori of *P. Polygoni-Convolvuli* are distinguished from those of *P. Polygoni-amphibii* by their compact pulvinate form, and by being soon uncovered by the epidermis, while the spores (perhaps in consequence of that) are much darker at the summit, and the apex, if conical, is less often oblique. According to Sydow these distinctions, however true they may be of the European forms of the species, do not avail when the extra-European forms are considered. In the Monographia, therefore, the two species are united, and only culture experiments will be able to decide the question.

99. *Puccinia Thesii* Chaill.

Æcidium Thesii Desv. in Journ. de Bot. ii. 311 p.p. Cooke, Handb. p. 537; Micr. Fung. p. 195, pl. 3, f. 50—1.

Puccinia Thesii Chaill. in Duby, Bot. Gall. ii. 889. Cooke, Handb. p. 495; Micr. Fung. p. 204. Plowr. Ured. p. 145. Sacc. Syll. vii. 602. Sydow, Monogr. i. 585. Fischer, Ured. Schweiz, p. 300, f. 219.

Spermogones. Amphigenous, numerous, amongst the *æcidia*.

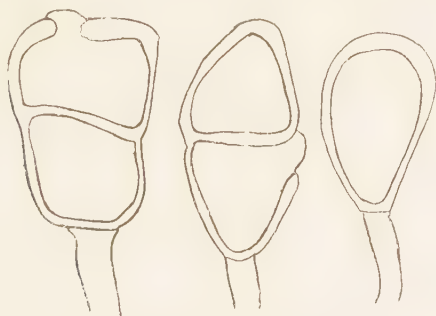


Fig. 177. *P. Thesii*. Telentospores, from a Surrey specimen.

Æcidiospores. *Æcidia* amphigenous, scattered uniformly and rather thickly over the whole leaf-surface, seldom in roundish

or oblong groups between cylindrical and cup-shaped, with a white torn recurved margin; spores delicately verruculose, orange, $16-24\ \mu$.

Uredospores. Sori amphigenous or on the stems, distributed irregularly, minute, roundish, long covered by the epidermis, brown; spores globose to broadly ellipsoid, verruculose, yellow-brown, $20-28\ \mu$, with four or five germ-pores.

Teleutospores. Sori similar, but more compact, brown-black; spores oblong to clavate, generally rounded above and slightly thickened, hardly or not at all constricted, rounded or attenuated below, smooth, uniformly brown, $35-54 \times 16-24\ \mu$; pedicels brownish, thick, not very persistent, short or as much as $9.5\ \mu$ long; a few mesospores intermixed.

On *Thesium humifusum*. Rare; Surrey, Dorset, Wilts., Hants., Cambs., etc. *Æcidia*, May—August (also recorded for October); teleutospores, August—October. (Fig. 177.)

It was maintained by Vuillemin (Bull. Soc. Myc. France, 1894, p. 107 ff.) that this species has no *æcidium*-stage, the *Æcidium Thesii* being referred by him to another species, *P. Descauxii* (= *P. Passerinii*), distinguished by its broader and warted teleutospores; but both Sydow and Fischer have disproved this contention. The *æcidia* are rather more common than the teleutospores, and are sometimes found among the teleuto-sori on the same leaf, in October.

DISTRIBUTION: Europe, Eastern Siberia.

100. *Puccinia Iridis* Wallr.

Uredo Iridis DC. Encycl. viii. 224. Plowr. Ured. p. 257.

Trichobasis Iridis Cooke, Micr. Fung. p. 227.

Puccinia Iridis Wallr. in Rab. Krypt. Fl. ed. i. p. 23 (1844). Plowr. Ured. p. 189. Sacc. Syll. vii. 657. Sydow, Monogr. i. 598. Fischer, Ured. Schweiz, p. 236, f. 186.

P. truncata B. and Br. Ann. Nat. Hist. ser. 2, xiii. 461 (1854). Cooke, Handb. p. 494; Micr. Fung. p. 203.

Uredospores. Sori amphigenous, solitary or somewhat aggregated, roundish or elongated, minute, long covered by the epidermis, not pulverulent, reddish-brown; spores globose to

ovate, ochraceous-brown, echinulate, $20-35 \times 16-26 \mu$; epispore thick, with 2—4 (or more) germ-pores.

Teleutospores. Sori hypophyllous, few and irregularly scattered, sometimes confluent, oblong, compact, persistent, soon naked, black; spores clavate or oblong, much thickened (up to 14μ) at the summit and rounded, less often conical or truncate, gently constricted, usually attenuated below, smooth, fuscous-brown, darker above, $30-52 \times 14-22 \mu$; pedicels brownish, thick-walled, persistent, about as long as the spore.

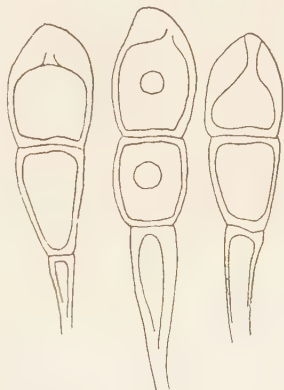


Fig. 178. *P. Iridis*. Teleutospores, on *I. Pseudacorus*.

On *Iris foetidissima*, *I. Pseudacorus*, and on many cultivated species of *Iris*. Not common. May—October; the teleutospores may be found on the old leaves until the following spring. (Fig. 178.)

The uredo-stage is most abundant and assumes various characters, especially as regards the formation of spots; when present these are conspicuous, oblong or oval, and yellowish, often with a greenish-brown circumference. In that case the leaf looks remarkably variegated.

Plowright considered that the form which occurs on our cultivated Irises is different from that on our native species, because he could not find any teleutospores in the former; other authors consider them as the same, because the teleutospores on many species are difficult to find, and appear only on dying leaves, especially towards the base, at the end of the season. One can easily recognise them by their being naked; for in this species, contrary to the usual state of things, the uredo-sori remain long concealed by the epidermis and the teleuto-sori soon become uncovered. The uredospores are very thick-walled; they can survive the winter and reproduce the fungus in the spring.

This species might be heterœcious: no experimental cultures appear to have been made. It will probably turn out to possess several biological races, for it has been recorded on more than thirty-five species of *Iris*.

DISTRIBUTION: Europe, Asia, North America.

101. **Puccinia Schroeteri** Pass.

Puccinia Schroeteri Pass. Nuov. Giorn. Bot. Ital. vii. 255. W. G. Smith, Gard. Chron. 1889, v. 725, f. 118. Wolley-Dod, Journ. Roy. Hort. Soc. xii. p. liii. Plowr. Trans. Brit. Myc. Soc. i. 57. Sacc. Syll. vii. 732. Sydow, Monogr. i. 608. Fischer, Ured. Schweiz, p. 78, f. 59.

Telentospores. Sori amphigenous, chiefly epiphyllous, large, oblong or elliptic, surrounded by a brownish-violet discoloration, 1—3 mm. long, solitary or in small clusters, long covered or half uncovered and surrounded by the lead-coloured epidermis,

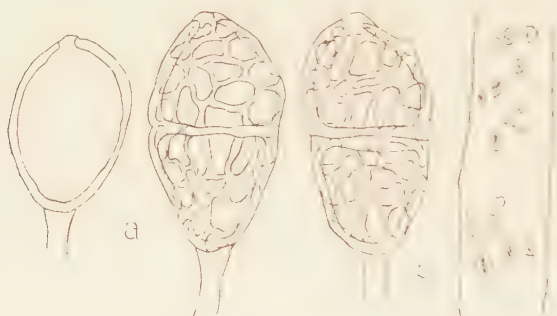


Fig. 179. *P. Schroeteri*. a, meso- and telentospore, from the original specimen of W. G. Smith; b, telentospore and sori on leaf of daffodil, from Cooke's specimen.

blackish-brown; spores ellipsoid or oblong, rounded at both ends, not thickened above, hardly constricted, obscurely reticulated, golden-brown, then chestnut, $40-60 \times 25-29 \mu$; pedicels hyaline, short, thick, deciduous; mesospores also occur.

On Jonquil and *Narcissus poeticus*. Very rare; Malpas, May, 1889 (Rev. C. Wolley-Dod); in Gard. Chron. and Journ. Roy. Hort. Soc. (*l.c.*) it is stated to have been found also on the "common double *Narcissus*" (? *N. telamonius plenus*). There are some specimens in Herb. Brit. Mus. on daffodil leaves, sent to the Gard. Chron. by a correspondent, May, 1894, and labelled *P. Liliacearum* by Cooke, which on examination prove to be this species. (Fig. 179.)

Plowright observed that the spores would not germinate at once, but, by securing the affected leaves during the winter near some plants of *N. poeticus*, he found the *Puccinia* reproduced next year and for eight or nine years afterwards, though only on the tips of the leaves. The reticulation of the spores varies in character, sometimes resolving itself into longitudinal ridges or rows of warts. Mesospores and other abnormal spores are recorded by Fischer.

DISTRIBUTION : Belgium, Italy, Carniola.

102. *Puccinia Asparagi* DC.

Puccinia Asparagi DC. Flor. fr. ii. 595. Cooke, Handb. p. 494 ; Micr. Fung. p. 203. Plowr. Ured. p. 144. Sacc. Syll. vii. 601. Sydow, Monogr. i. 615. Fischer, Ured. Schweiz, p. 235, f. 185.

Spermogones. In little clusters, honey-yellow.

Æcidiospores. *Æcidia* in oblong groups on the stems, for a long time closed, then shortly cup-shaped, with a whitish, erect, torn margin ; spore delicately verruculose, orange, $15-28\ \mu$.

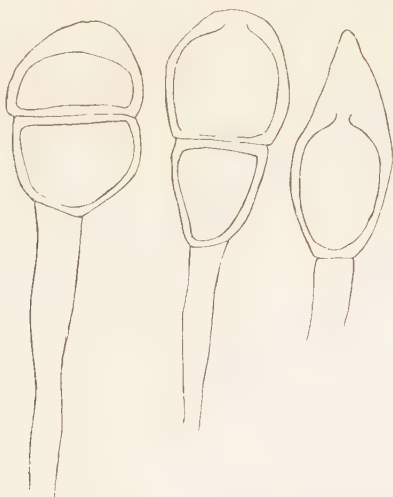


Fig. 180. *P. Asparagi*. Teleutospores and mesospore.

Uredospores. Sori oblong, narrow, flat, long covered by the epidermis, cinnamon-brown ; spores globose to ovate, delicately and densely echinulate, pale-brown, $20-30 \times 17-25\ \mu$, with four germ-pores.

Teleutospores. Sori oblong or linear, often confluent, generally on the stems, rarely on the leaves (phylloclades), blackish-brown; spores ellipsoid to clavate, thickened (up to 8μ) and rounded above, very gently constricted, rounded below, smooth, brown, $35-52 \times 17-26\mu$; pedicels hyaline or brownish, persistent, as long as or longer than the spore; a few obovate mesospores intermixed.

On *Asparagus officinalis*. *Æcidia*, not common, May; uredo- and teleutospores, September—December, rather frequent. (Fig. 180.)

Fischer points out that the connection between the *æcidium* and the other spore-forms has not yet been demonstrated. This disease is often very destructive to asparagus beds; all diseased shoots should be gathered and burnt. The best means of prevention is by the selection of resistant varieties, and the avoidance of overcrowding.

DISTRIBUTION: Europe, Abyssinia, North America.

103. *Puccinia Liliacearum* Duby.

Puccinia Liliacearum Duby, Bot. Gall. ii. 891. Plowr. Ured. p. 197. Sacc. Syll. vii. 668. Sydow, Monogr. i. 627. Fischer, Ured. Schweiz, p. 76, 545, f. 57.

Spermogones. Numerous, especially at the apex of the affected leaves, yellowish, conical.

[*Æcidiospores.* *Æcidia* few, scattered, minute, deeply immersed, whitish, the narrow opening only projecting; spores minutely verruculose, orange, about $15-20\mu$.]



Fig. 181. *P. Liliacearum*. Teleutospore (*Lythrum*).

Teleutospores. Sori amphigenous, embedded in the dried yellowish parts of the leaf, hemispherical, densely crowded, often confluent, long covered by the ashy-grey epidermis which at length opens by a cleft, then naked, pulverulent, reddish-brown; spores oblong-fusiform or clavate, not thickened above and rounded or frequently somewhat narrowed, not constricted, indeed broadest at the septum, attenuated below, smooth, pallid-brown, $40-75 \times 22-35\mu$; pedicels hyaline, thick, rather long.

On *Ornithogalum umbellatum*. Rare; Lytham and near Carlisle (Rev. Hilderic Friend). March—May. (Fig. 181.)

As usual, only spermogones and teleutospores are present on these specimens. Fischer records that he found the fungus on *O. umbellatum* in March and April in great plenty, with spermogones and teleutospores, but no æcidia; the infested parts of the leaves were swollen, compact, and harder than the healthy portions. He suggests (Centralbl. f. Bakt. 2. xv. 230) with great probability that the æcidia with spermogones which are also found on *Ornithogalum* (*Æcidium ornithogaleum* Bubák, Annal. Myc. iii. 222) belong to some heterœcious species. The fungus on *O. umbellatum* is a biologic race; it does not attack *O. nutans*, much less other allied species of Liliaceæ, such as *Muscari* and *Hyacinthus*, although *P. Liliacearum* is recorded on them. Fischer adds that the mycelium is not perennial, but infection takes place afresh each spring by the basidiospores of the overwintered teleutospores, from leaves lying on the ground.

DISTRIBUTION: Central Europe.

104. *Puccinia Porri* Wint.

Uredo Porri Sow. Engl. Fl. pl. 411.

U. Alliorum DC. Flor. fr. vi. 82 p.p. Cooke, Handb. p. 528; Micr. Fung. p. 217 p.p.

Uromyces Alliorum DC.; Cooke, Handb. p. 518; Micr. Fung. p. 212. Plowr. Ured. p. 137 p.p.

Puccinia Porri Wint. Pilze, p. 200. Plowr. Ured. p. 148. Sacc. Syll. vii. 605. Sydow, Monogr. i. 610. Fischer, Ured. Schweiz, p. 80, f. 61.

Uredospores. Sori amphigenous, on indeterminate pallid spots, scattered or more or less in rows, minute, at first covered by the swollen epidermis, yellowish or reddish-yellow; spores globose to ellipsoid, very delicately echinulate, yellowish, 20—30 μ .

Teleutospores. Soriamphigenous or cauliculous, generally without spots, scattered, minute, oblong or roundish, about 1 mm. wide, but sometimes confluent into larger patches, long covered by the lead-coloured epidermis, black-brown; spores oblong or clavate, rounded or rather truncate



Fig. 182. *P. Porri*. Teleutospores and mesospore, on *A. Schoenoprasum*.

above, scarcely or slightly thickened, gently constricted, rounded or apiculate below, smooth, brown, $28-52 \times 20-26 \mu$; pedicels hyaline, short, deciduous; mesospores numerous, obovate or pyriform, very irregular, $22-36 \times 15-23 \mu$.

On leaves, sheaths and stems of various species of *Allium*, *A. Cepa*, *A. Schoenoprasum*, *A. Scorodoprasum*, etc. Rather uncommon. June—August. (Fig. 182.)

Fischer describes the uredospores as pale-brown, distantly warted, $28-32 \times 21-28 \mu$, and provided with three germ-pores. The æcidium on *Allium* which is usually placed with this species does not belong here. The æcidium on *Allium ursinum* is known to belong to one of the forms of *P. sessilis*: some, if not all, of the æcidia on other species of *Allium* may be in the same class. It was Tranzschel (Ann. Mycol. 1910, viii. 415) who proved that *P. Porri* is a Hemipuccinia; he sowed the basidiospores on *Allium* and obtained the uredospores direct. The supposed æcidium is almost always found separate from the uredo- and teleutospores. There is a very close alliance between *P. Porri* and *Uromyces ambiguus*, if indeed they are not the two extremes of the same species.

If this disease attacks cultivated onions, as it sometimes does, remove and burn all diseased plants and do not sow onions on the same ground again for several years.

DISTRIBUTION: Europe, Syria.

105. *Puccinia obscura* Schröt.

Æcidium Compositarum var. *Bellidis* DC.; Cooke, Handb. p. 543.

Puccinia obscura Schröt. in Nuov. Giorn. Bot. Ital. ix. 256. Plowr. Ured. p. 174; Grevillea, xii. 86. Sacc. Syll. vii. 629. Sydow, Monogr. i. 645, 898. Fischer, Ured. Schweiz, p. 237, f. 187.

Spermogones. Amphigenous, minute, in dense roundish clusters, honey-coloured.

Æcidiospores. Æcidia amphigenous, on roundish or irregular yellow spots, in loose clusters or scattered, between cup-shaped and cylindrical, with whitish torn margin; spores delicately verruculose, yellowish, $16-22 \mu$.

Uredospores. Sori generally hypophyllous, on irregular confluent purplish-brown spots, scattered, elliptical or linear, long covered by the epidermis, pulverulent, rusty-yellow;

spores ellipsoid to ovate, echinulate, pale-brown, $18-26 \times 15-22 \mu$; epispore rather thick, with two germ-pores.

Teleutospores. Sori similar, but compact, pulvinate, covered or surrounded by the cleft epidermis, blackish-brown; spores

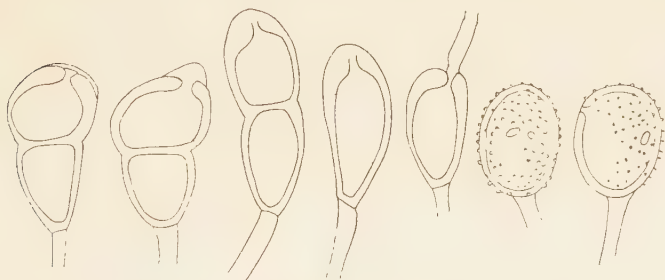


Fig. 183. *P. obscura*. Teleutospores; two mesospores, one germinated in the sorus; and two uredospores; all on *L. campestris*.

oblong, rounded, rarely truncate or conical above and thickened ($5-9 \mu$), gently constricted, usually attenuated below, smooth, brown, $30-48 \times 14-20 \mu$; pedicels subhyaline, persistent, up to 30μ long; mesospores frequently intermixed with the teleutospores.

Æcidia on *Bellis perennis*, September—December; uredo- and teleutospores on *Luzula campestris*, *L. silvatica*. June—November. Not common, except locally. (Fig. 183.)

Teleutospores are rarely produced, and I have seen them only on dead leaves; the fungus can winter by its uredospores, and in such cases, of course, the æcidium will not be formed. It is probably in consequence of this that the æcidia and the uredospores are frequently not found near one another; there is a great difference in their mode of occurrence in different districts. The uredospores sometimes show a small smooth spineless area just below the germ-pores. Fischer records them in Switzerland on *Luzula maxima* and *L. pilosa* in September, and Sydow includes all the species (except *L. arcuata*) which grow in Britain.

The heterœcism of this parasite was first demonstrated by Plowright; the æcidia differ from nearly all others in being produced in late autumn and winter. According to him, the teleutospores, when they occur, are not formed till August and September, and germinate after a short resting period; thus the succeeding phase arises on the Daisy usually about October. I have found that the spermogones (which are not mentioned by

other authors appear first on yellow spots, and are slowly followed by the æcidia towards November or earlier; at that time of the year the Daisy plants are generally in a condition of vigorous, though slow, growth.

There is a species of *Puccinia* (*P. distincta* McAlp.) found on *Bellis perennis* in Australia, but this bears æcidia and teleutospores on the same leaves; there are no uredospores. Since the Daisy is not a native of that country and is grown there from seed imported from England and Germany, it would seem that the fungus is imported with the seed; yet in our country and in Germany, the Daisy never bears teleutospores. The teleutospores of the Australian species closely resemble those of *P. obscura* on *Luzula*, and like them are often intermixed with numerous mesospores; moreover, they often grow amongst and round the æcidia, apparently always from the same mycelium. Can it be that the European fungus has been introduced with the seed and has adapted itself to an autoëcious life? This, however, seems hardly probable, since *Luzula campestris* is found in Australia, but the *Puccinia* which attacks it there (*P. tenuispora* McAlp.) is different from either of our European species.

DISTRIBUTION: Central and Northern Europe, North America.

106. *Puccinia oblongata* Wint.

Caeoma oblongatum Link, Obs. Myc. ii. 27.

Trichobasis oblongata Berk.; Cooke, Handb. p. 529; Micr. Fung. p. 223, pl. 7, f. 158—9.

Puccinia Luzulae Lib.; Cooke, Grevillea, iv. 109; Micr. Fung. p. 203.

P. oblongata Wint. Pilze, p. 183. Plowr. Ured. p. 190. Sacc. Syll. vii. 658. Sydow, Monogr. i. 646. Fischer, Ured. Schweiz, p. 239, f. 188.

Uredospores. Sori amphigenous, on irregular and confluent reddish-brown or blackish-brown spots, scattered, oblong, long covered by the epidermis, ferruginous; spores oblong-ovate to pyriform or clavate, irregular, smooth, rarely aculeolate at the summit, rusty-yellow, $30-44 \times 12-15 \mu$; epispore colourless, thick, without germ-pores.

Teleutospores. Sori similar, but soon naked, compact, blackish-brown; spores clavate, much thickened ($10-25 \mu$) above where they are rounded or rarely more or less obliquely tapering, gently constricted, tapering gradually downwards, smooth, brown, $44-80 \times 16-24 \mu$; pedicels hyaline, persistent, about as long as the spore or shorter.

On *Luzula campestris*, *L. marima*, *L. pilosa*. Uredospores, May—July; teleutospores, September—November. (Fig. 184.)

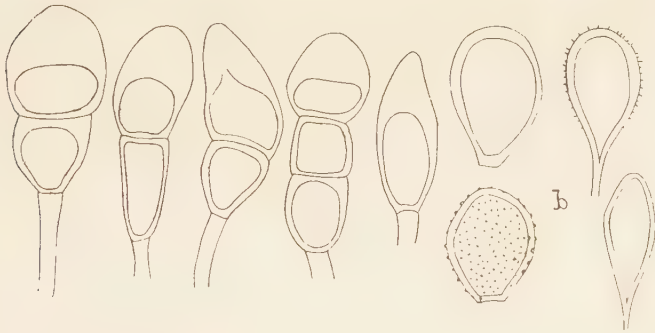


Fig. 184. *P. oblongata*. Teleutospores (one abnormal) and a mesospore; b, uredospores; all on same leaf of *L. pilosa*.

The uredospores are said to be always smooth; more or less obovate, and often irregular. It is stated by Sydow that they can survive the winter. Fischer figures anomalous spores, of both kinds, including three-celled and one-celled teleutospores.

Plowright's suggestion that this is probably a heterœcious species has, so far, received not the slightest confirmation. The greatly thickened summit of the teleutospores is very striking; they are produced in the old uredo-sori, especially towards the tip of the leaves, so that in a sorus which is producing uredospores a few young teleutospores may be found, and the fully-formed ones are surrounded by the numerous persistent uredospore-pedicels.

It is, no doubt, very heterodox, but I cannot help expressing the opinion that *P. oblongata* is merely an abnormal development of *P. obscura*. On the same leaf of *Luzula pilosa*, if not in the same sorus, I have found almost all the various kinds of spores figured by Fischer under both species. *Uredo oblongata* Grev. Scot. Crypt. Flor. pl. 12, doubtless includes this form, but his figure is *P. Caricis*.

DISTRIBUTION: Central and Northern Europe.

107. *Puccinia Scirpi* DC.

Æcidium Nymphoidis DC. Flor. fr. ii. 597 and vi. 93. Plowr. Gard. Chron. 1895, xviii. 96, 135.

Puccinia Scirpi DC. Flor. fr. ii. 223. Plowr. Ured. p. 191. Sacc. Syll. vii. 659. Sydow, Monogr. i. 688. Trans. Brit. Myc. Soc. i. 58. Fischer, Ured. Schweiz, p. 298, f. 218.

Spermogones. Epiphyllous, in roundish clusters.

Aecidiospores. Aecidia epiphyllous, on roundish yellow spots, in orbicular clusters as much as 1 cm. diam. surrounding a group of spermogones, scutelliform, yellow, with a slightly and irregularly torn narrow margin; spores delicately verruculose, orange, $12-20\ \mu$.

Uredospores. Sori scattered or in rows, often confluent, oblong, elliptical or linear, long covered by the swollen epidermis which is at length longitudinally split, ferruginous; spores subglobose to ovoid, often flattened on one side, echinulate, pale-brown, $19-32 \times 12-24\ \mu$, with two germ-pores.

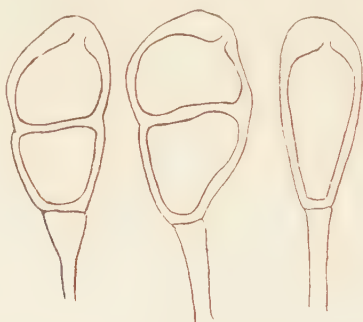


Fig. 185. *P. Scirpi*. Teleutospores and mesospore, from the original specimens, King's Lynn (ex herb. Plowright).

Teleutospores. Sori similar, generally numerous and confluent, black-brown; spores oblong or subclavate, thickened above ($5-9\ \mu$) and rounded, truncate, or subconical, hardly constricted, attenuated downwards, smooth, brown, $30-60 \times 12-24\ \mu$; pedicels yellowish, persistent, $25-45\ \mu$ long; mesospores more or less abundant, $24-40\ \mu$ long.

Aecidia on leaves of *Limnanthemum* (*Villarsia*) *nymphaeoides* (*Nymphoides peltatum*), July; uredo- and teleutospores on culms of *Scirpus lacustris*, July—November. Rare; King's Lynn; near Earith (Huntingdonshire). (Fig. 185.)

Plowright suggested in 1889 (Monograph, p. 191) that this *Puccinia* was most likely a heteroecious species. Chodat was led, in 1891, to suspect the *Limnanthemum* as the alternate host, by finding the two stages both together in the same pond in the Botanic Gardens at Geneva. Klebahn

had the same experience at Bremen. Bubák experimentally demonstrated the truth of the suspicion (Österr. Bot. Zeitschr. 1898, xlviii. 14).

The teleutospores were first found, in this country, on *Scirpus lacustris* floating down the river Ouse at King's Lynn, Nov. 17, 1877. The plants had evidently been cut on that river or one of its tributaries, but it was not till 1894 that the teleutospores were found *in situ* near Earith, Huntingdonshire; and a visit to the Old Bedford Level at that place, in July, 1895, revealed the æcidia in abundance. See Gard. Chron. (l. c.).

DISTRIBUTION: Europe generally; a similar æcidium on *Limnanthemum indicum* has been found in Queensland, but no teleutospores have yet been found there.

108. *Puccinia Caricis* Reb.

Æcidium Urticæ Schum. Enum. Pl. Säll. ii. 222. Cooke, Handb. p. 541; Micr. Fung. p. 197, pl. 1, f. 10, 11.

Uredo Caricis Schum. l. c. p. 231.

Trichobasis caricina Berk.; Cooke, Micr. Fung. p. 223, pl. 8, f. 170—1.

Puccinia Caricis Rebert. Fl. Neom. p. 356. Plowr. Ured. p. 169.

Sacc. Syll. vii. 626. Sydow, Monogr. i. 648. Fischer, Ured.

Schweiz, p. 265, f. 201. McAlpine, Rusts of Australia, p. 133, f. 29, 30.

P. striola Link, Sp. Pl. p. 67. Cooke, Handb. p. 493; Micr. Fung. p. 203 p.p.

Spermogones. Epiphyllous, in small clusters, honey-coloured.

Æcidiospores. Æcidia hypophyllous or occasionally amphigenous, often on the petioles and stems, on reddish, yellow or purplish spots, in dense clusters of various sizes which are often very large and cause great swelling and distortion on the stems, cup-shaped, with torn white recurved margin; spores verruculose, orange, $16-26 \times 12-20 \mu$.

Uredospores. Sori amphigenous, generally hypophyllous, scattered, oblong, about $\frac{1}{2}$ mm. long, pale-brown; spores subglobose to oval, echinulate, yellow-brown, $21-30 \times 15-22 \mu$, with three (rarely four) germ-pores.

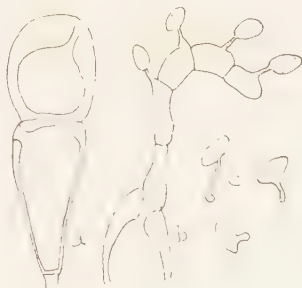


Fig. 186. *P. Caricis*. *a*, teleutospore; *b*, upper cell germinating; *c*, basidiospores germinating.

Teleutospores. Sori generally hypophyllous, scattered or arranged in lines, oblong or linear and confluent into long striae, pulvinate, compact, black; spores clavate, usually rounded above and much thickened ($5-10\mu$), constricted, tapering downwards, smooth, brown, darker at the apex, $35-66 \times 14-23\mu$; pedicels yellowish, persistent, about half as long as the spore or less.

Æcidia on *Urtica dioica*, April—June; uredo- and teleutospores on *Carex acutiformis* (*pubulosa*), *C. hirta*, *C. pendula*, *C. Pseudocyperus*, *C. riparia*, June or July—April. Very common. (Fig. 186.)

It is recorded also, in other countries, upon a long series of other *Carices* (over forty-three), including *C. acuta*, *C. Goodenoviï*, *C. stricta*, and *C. vesicaria* among British species. It must not be assumed, however, without trial that these are all identical; the forms on *C. hirta*, *C. vesicaria* seem to be biologically distinct (Klebahn, Fischer), and others may belong to *P. Pringsheimiana*, etc. *C. binervis* is included by Plowright, but the fungus on this host has not yet been experimentally shown to belong to *Æ. Urticae*.

This parasite has been the subject of numerous investigations, since Magnus in 1872 first showed that the æcidium on the Nettle belonged to the life-cycle of *P. Caricis* on *Carex hirta*. Plowright, Schröter, Klebahn, and many others have followed in his steps. It may be remarked here that few species of *Puccinia* on *Carex* can be determined with certainty until the æcidium-stage belonging thereto is known.

The teleutospores of this species germinate after the winter's rest; they succeed most easily during April. They may be found on new or old leaves of *Carex* all the year round. It is almost in vain to look for the æcidium on the Nettle except in the vicinity of water where Sedges are growing; but where such a conjunction occurs, the parasite may often be found upon both hosts in abundance every year. Klebahn records the æcidium on *Urtica urens*; Magnus states that the fungus can winter on *C. hirta* by means of its uredospores.

DISTRIBUTION: Europe, Siberia, Japan, America, Australia.

109. *Puccinia Pringsheimiana* Kleb.

Æcidium Grossulariae DC. Flor. fr. vi. 92. Cooke, Handb. p. 541; Mier. Fung. p. 197. Plowr. Ured. p. 263.

Puccinia Pringsheimiana Kleb. in Zeitschr. f. Pflanzenkr. v. 76. Soppitt in Gard. Chron. 1898, xxiv. 145, f. 38. Sydow, Monogr. i. 652. Fischer, Ured. Schweiz, p. 268. Masee, Diseases of cultivated Pl. p. 300, f. 88.

Æcidiospores. *Æcidia* hypophyllous, crowded on red and yellow spots, roundish, also in elongated clusters on the young branches, petioles, and nerves, sometimes entirely covering the young fruits, shortly cylindrical, with broad, recurved, white, much torn margin; spores orange, verruculose, $15-21 \times 14-18 \mu$.

Uredospores. Sori hypophyllous, punctiform, about $\frac{1}{2}$ mm. long, on yellowish spots; spores more or less globose, pale-brown, echinulate, $18-22 \times 17-21 \mu$, with three, rarely four, germ-pores.

Teleutospores. Sori amphigenous, linear or punctiform, up to 1 mm. long, pulvinate, brownish-black; spores resembling those of *P. Caricis*, $40-58 \times 15-22 \mu$.

Æcidia on *Ribes Grossularia*, *R. nigrum* (?), May and June, common; uredo- and teleutospores on *C. acuta*, *C. caespitosa*, *C. Goodenowii*, *C. stricta*. (Fig. 187.)



Fig. 187. *P. Pringsheimiana*.
Leaf of *Ribes Grossularia*
with groups of *æcidia*.

The teleutospore-hosts are those given by Klebahn and Fischer. Klebahn first suggested the connection of the æcidium with a *Puccinia* on *Carex*, and has since demonstrated the truth of this idea by many culture experiments. Soppitt also showed the same for *Carex acuta* and *C. Goodenowii*. The æcidium is said to attack *R. alpinum*, *R. aureum*, *R. rubrum*, *R. sanguineum*, but less frequently. Plowright records the æcidium on leaves of *Ribes nigrum* (Norfolk, June, 1890), but there is no proof that it belonged to this species.

This species is one of those forms originally named by Klebahn *P. Ribesii-Caricis*; he has since divided them under five heads which can scarcely be reckoned anything but biological races:—*P. Pringsheimiana*, *P. Ribis-nigri-Acutae*, *P. Ribis-nigri-Paniculatae*, *P. Pseudo-cyperii*, and *P. Magnusii* (the latter on *C. acutiformis* and *C. riparia*). The same species of *Ribes* serve as alternate hosts in each case, in varying degrees of susceptibility, except that *P. Magnusii* is not recorded for *R. rubrum* and *R. Grossularia*. The morphological differences between these forms are slight and elusive.

P. Pringsheimiana can be distinguished from *P. Caricis* by its nearly

round uredospores, but most of the other biological races of *P. Ribesii-Caricis* have them oval or oblong. There is no remedy for this disease on the Gooseberry but to gather and burn all diseased leaves and fruit, etc., and even this will be of no avail so long as the affected *Carices* continue to exist. Luckily the disease rarely does much harm.

110. *Puccinia dioicæ* Magn.

Æcidium Cirsii DC. Flor. fr. vi. 94.

Puccinia dioicæ Magn. Tag. Nat. Vers. München, 1877, p. 200. Plowr.

Ured. p. 173. Sacc. Syll. vii. 629. Sydow, Monogr. i. 653.

Fischer, Ured. Schweiz, p. 283, f. 208.

Spermogones. In little clusters, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous, on roundish yellow or brownish spots, in clusters 2—5 mm. diam., cup-shaped, with torn white margin; spores delicately verruculose, orange, 18—25 μ .



Fig. 188. *P. dioicæ*.
Æcidia on *C. pratense*,
co. Mayo (J. Adams),
nat. size.

[*Uredospores.* Sori scattered, minute punctiform, brown; spores globose to ellipsoid, echinulate, pale-brown, 18—25 μ .

Teleutospores. Sori scattered, roundish or oblong, 1 mm. long, soon naked, surrounded by the cleft epidermis, pulvinate, black; spores clavate, rounded or conical and much thickened (up to 14 μ) above, gently constricted, tapering below, smooth, brown, darker at the apex, 35—56 $\times$ 14—20 μ , occasionally 70 μ long; pedicels brownish, persistent, as much as 50 μ long.]

Æcidia on *Cirsium palustre*, *C. pratense*, and (on the continent) on other species of *Cirsium*, June, July; uredo- and teleutospores on *Carex dioica*, *C. Davalliana* (?). Very rare; Scotland, Ireland. I have not seen the teleutospores. (Fig. 188.)

DISTRIBUTION: Northern parts of Europe.

111. *Puccinia silvatica* Schröt.

Æcidium Taraxaci K. et S. Myk. Heft. i. 85.

Puccinia silvatica Schröt. in Cohn, Beitr. iii. 68. Plowr. Ured. p. 172.

Sacc. Syll. vii. 627. Sydow, Monogr. i. 656. Fischer, Ured.

Schweiz, p. 289, f. 211.

Spermogones. In little clusters, yellowish.

Æcidiospores. *Æcidia* hypophyllous or amphigenous, on roundish yellow or brown spots, in crowded clusters 2—5 mm. wide, rarely solitary, occasionally on the peduncle which they distort, cup-shaped, with torn whitish revolute margin; spores nearly smooth, orange, 14—21 μ .

[*Uredospores*. Sori hypophyllous, scattered, minute, oblong, brown; spores globose to ovate, echinulate, brown, 20—27 $\times$ 15—22 μ .

Teleutospores. Sori hypophyllous, scattered, minute, roundish or oblong, reaching 1 mm. in length, pulvinate, black; spores clavate, rounded and much thickened (up to 11 μ) above, rarely conically attenuated, gently constricted, tapering below, smooth, pale-brown, darker at the apex, 35—55 $\times$ 12—18 μ ; pedicels brownish, persistent, as much as 40 μ long.]

Æcidia on *Taraxacum officinale*, June, July. I have seen specimens from both England and Ireland. Teleutospores on species of *Carex*. (Fig. 189.)



Fig. 189. *P. silvatica*. *Æcidia* on leaf of *Taraxacum*, from one of Soppitt's specimens, Saltaire.

The question whether *P. silvatica* occurs in Britain is still in the same state as in Soppitt's time. The *æcidium* agrees with the one assigned to that species, but the teleutospores have not been found; there is no evidence that those found on *Carex remota* at Kew belonged to this species. The distinction of this *æcidium* from that belonging to *P. variabilis* lies chiefly in the clustered peridia, which are situated on a thickened part of the leaf, the peridium-cells are arranged in evident rows and the spores form, according to Juel, longer chains. Fischer insists that the peridium cells are thickest on the outer side, while those of *P. variabilis* are thickest on the inner side: he maintains that this difference is characteristic of

heteroecious and autoecious species respectively, though this is certainly not always true.

The only British species of *Curea* which have been proved by cultures to be connected with this aecidium are *C. caryophyllea* (*praecox*) and *C. arenaria*, but it is supposed to grow also on a large number of other species. The matter is, however, complicated by the fact that there are two other *Puccinia* (*P. arenariicola* and *P. Schoeleriana*) which are very closely allied and differ chiefly in having their aecidia on other hosts.

DISTRIBUTION: Europe and Siberia.

112. *Puccinia Schoeleriana* Plowr. et Magn.

Aecidium Jacobaeae Grev. Flor. Edin. p. 445.

A. Compositarum var. *Jacobaeae*; Cooke, Handb. p. 542; Mier. Fung. p. 198 p.p.

A. Senecionis Fischer, Ured. Schweiz, p. 534, f. 335 (?).

Puccinia Schoeleriana P. et M. Quart. J. Micr. Sci. xxv. (new ser.) pp. 167, 170. Phill. et Plowr. Grevillea, xiii. 54. Plowr. Journ. Linn. Soc. xxiv. 91; Ured. p. 171. Sacc. Syll. vii. 627. Sydow, Monogr. i. 659.

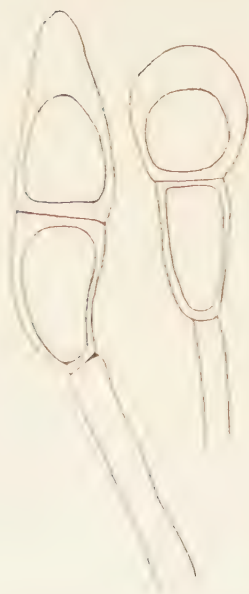


Fig. 190. *P. Schoeleriana*.
Teliospores, from one of
Plowright's cultures on *C.*
arenaria.

Spermogones. Epiphyllous, orange.

Aecidiospores. Aecidia hypophyllous, clustered on roundish yellow or brownish spots as much as 1 cm. diam., cup-shaped, with a torn white reflexed margin; spores delicately echinulate, orange, 15—21 μ .

Uredospores. Sori generally hypophyllous, on yellowish spots, scattered, minute, roundish or oblong, pulverulent, surrounded by the cleft epidermis, pale-brown; spores globose to ovate, echinulate, yellow-brown, 24—30 $\times$ 16—25 μ .

Teliospores. Sori hypophyllous, scattered or aggregated, $\frac{1}{2}$ —1 $\frac{1}{2}$ mm. long, oblong, surrounded by the torn epidermis, pulvinate, black; spores clavate or fusoid, rounded or conically attenuated above and much thickened (up to 14 μ), gently constricted, tapering

downwards, smooth, brown, darker at the apex, $45-80 \times 18-22 \mu$; pedicels brownish-yellow, persistent, $25-40 \mu$ long.

Æcidia on *Senecio Jacobaea*, May and June; uredo- and teleutospores on *Carex arenaria*, July—May. Rare; Norfolk, Lincolnshire, Aberdeen, Burntisland. (Fig. 190.)

The life-history of this parasite was investigated by Plowright, who at the same time demonstrated by his experimental cultures its distinctness from *Puccinia Caricis* and *P. arenariicola*. Fischer records (*l.c.*) an æcidium on *Senecio Jacobaea*, *S. aquaticus* and *S. erucifolius* closely resembling this, but points out at the same time that *C. arenaria* does not grow in Switzerland; if, therefore, it is the same fungus, as it seems without doubt to be, its alternate stage must occur there on some allied species of *Carex*, such as *C. disticha*.

DISTRIBUTION: Germany, Holland, Switzerland (?), Russia.

113. *Puccinia arenariicola* Plowr.

Puccinia arenariicola Plowr. Journ. Linn. Soc. Bot. xxiv. 90; Ured. p. 170. Sacc. Syll. ix. 311. Sydow, Monogr. i. 661.

Æcidiospores. Æcidia generally hypophyllous, in round clusters on circular yellow spots which are as much as 1 cm. diam. and margined with purple, cup-shaped, yellowish, with torn revolute margin; spores nearly smooth, yellow, $15-20 \mu$.

Uredospores. Sori on yellowish spots, linear or oblong, surrounded by the torn epidermis, brown; spores globose to ovate, delicately echinulate, pale-brown, $18-22 \mu$.

Teleutospores. Sori generally hypophyllous, scattered or sometimes aggregated, oblong, as much as 1 mm. long, pulvinate, black; spores clavate or oblong-clavate, rounded above where they are darker and much thickened (14μ), gently constricted, tapering downwards, smooth, brown, $40-65 \times 14-22 \mu$; pedicels brownish, persistent, as much as 40μ long.



Fig. 191. *P. arenariicola*. Æcidia on leaf of *Centaurea nigra*, produced artificially in one of Plowright's cultures (reduced).

Æcidia on *Centaurea nigra*, May and June; uredo- and teleutospores on *Carex arenaria*, July—April. Very rare; on the sea-shore, Hemsby, Norfolk. (Fig. 191.)

It has not been found anywhere else: but in all probability it could fairly be regarded as merely a well-marked biological race or mutation of *P. Schoeleriana* (q.v.). Plowright's suggestion that it is identical with *P. tenuistipes* Rost. seems less likely, but it is closely allied to *P. Caricis-montanae* Fisch.

114. *Puccinia extensicola* Plowr.

Puccinia extensicola Plowr. Ured. p. 181. Sacc. Syll. ix. 311. Sydow, Monogr. i. 667.

Æcidiospores. *Æcidia* amphigenous or on the stems, seated on paler spots, scattered or in clusters, cup-shaped, whitish-yellow, with torn margin; spores delicately verruculose, pale-orange, $16\text{--}22\ \mu$.

Uredospores. Sori on extensive pale spots, scattered, minute, oblong or linear, reddish-brown; spores subglobose or ovate, irregular, very delicately echinulate, yellowish-brown, $22\text{--}30 \times 16\text{--}22\ \mu$.

Teleutospores. Sori oblong, $\frac{1}{2}\text{--}1$ mm. long, covered for a long time by the epidermis which at length splits, pulvinate, black; spores subclavate, rounded or truncate above, rarely hooded, thickened (up to $8\ \mu$), gently constricted, tapering downwards, smooth, brown, $40\text{--}60 \times 18\text{--}24\ \mu$; pedicels short, hyaline; a few mesospores occasionally intermixed.

Æcidia on *Aster Tripolium*, June, July; uredo- and teleutospores on *Carex extensa*, August—June. Rare; Wells, Norfolk.

The life-history of this species was worked out by Plowright in 1888; it has hardly been found elsewhere except in Istria.

115. *Puccinia paludosa* Plowr.

Æcidium Pedicularis Libosch, Mém. Moscou, v. 76, pl. 5, f. 1. Cooke, Handb. p. 544; Micr. Fung. p. 199.

Puccinia paludosa Plowr. Ured. p. 174. Sacc. Syll. ix. 311. Sydow, Monogr. p. 671. Fischer, Ured. Schweiz, p. 273, f. 203.

Spermogones. In little clusters, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous or on the more or less swollen petioles and stems, clustered in round elongated or irregular groups, cup-shaped, with torn white revolute margin; spores delicately verruculose, pallid-orange, $15-25\ \mu$.

Uredospores. Sori hypophyllous, on yellowish spots, scattered or in little groups, very minute, roundish or oblong, soon naked, pulverulent, yellowish-brown; spores more or less globose, delicately echinulate, brownish, $20-26\ \mu$.

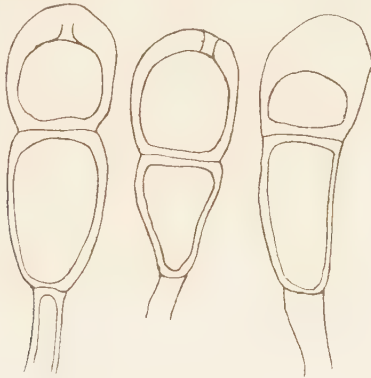


Fig. 192. *P. paludosa*. Teleutospores on *C. vulgaris*, Norfolk.

Teleutospores. Sori hypophyllous, minute, scattered or arranged in long lines, pulvinate, quite black; spores clavate, rounded above and strongly thickened (up to $11\ \mu$), constricted, tapering below, smooth, brown (upper cell very dark), $45-60 \times 16-22\ \mu$; pedicels brownish, persistent, rather long.

Æcidia on *Pedicularis palustris*, June, July; uredo- and teleutospores on *Carex fulva*, *C. panicea*(?), *C. stricta*, *C. vulgaris* (*Goodenovi*), from July onwards. As usual on *Carex*, the teleutospores can be found throughout the winter. Rare: Norfolk, Orkney. (Fig. 192.)

DISTRIBUTION: Central and Northern Europe.

116. ***Puccinia uliginosa*** Juel.

Æcidium Parnassiae Gravis, in Bot. Gall. ii. 904. Cooke, Micr. Fung. p. 198; Grevillea, i. 8 and ii. 161. Plowr. Ured. p. 129. Irish Naturalist, Oct. 1907, p. 321.

Puccinia uliginosa Juel, Öfvers. k. Vetensk.-Akad. Förh., 1894, no. 8, p. 410. Sacc. Syll. xi. 198. Sydow, Monogr. p. 673. Fischer, Ured. Schweiz, p. 267, f. 202.

Æcidiospores. *Æcidia* hypophyllous, clustered on yellow, then brown circular spots 2—5 mm. diam., or sometimes occupying the whole leaf-surface, cup-shaped, with torn recurved yellowish margin; spores delicately verruculose, orange, 14—18 μ .

[*Uredospores.* Sori amphigenous, scattered, very minute, rounded or oblong, pulverulent, yellow-brown; spores globose to ovate, echinulate, brownish, 21—25 μ , with three germ-pores.

Teleutospores. Sori amphigenous or in little groups, minute, punctiform, roundish or oblong, pulvinate, black; spores oblong or somewhat clavate, rounded above and thickened (up to 8 μ), gently constricted, rounded or attenuated below, smooth, brown, darker at the apex, 30—38 $\times$ 12—18 μ ; pedicels subhyaline, persistent, 15—32 μ long.]

Æcidia on *Parnassia vulgaris*, June; uredo- and teleuto-spores on *Carex vulgaris* (*Goodenovii*) and its var. *juncella*. Only the *æcidium* recorded for Britain; Glasgow, Aberdeen, Ireland.

117. *Puccinia graminis* Pers.

Æcidium Berberidis Gmel.; Cooke, Handb. p. 538; Micr. Fung. p. 195.

Trichobasis linearis Lév.; Cooke, Micr. Fung. p. 223, pl. 7, f. 144.

P. graminis Pers. Disp. Meth. p. 39. Cooke, Handb. p. 493; Micr. Fung. p. 202. Plowr. Ured. p. 162. Sacc. Syll. vii. 622. Sydow, Monogr. i. 692. Fischer, Ured. Schweiz, p. 243, f. 190. McAlpine, Rusts of Australia, p. 120, and many figures.

Spermogones. In little clusters, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous, often also on the fruit, on roundish, often thickened spots, 2—5 mm. diam., which are margined with reddish-purple or yellow, clustered or scattered, cylindrical, white, with a cut and somewhat erect margin; spores appearing smooth, verging on orange, 14—26 μ diam.

Uredospores. Sori amphigenous, often also on the sheaths and culms, scattered or arranged in rows, linear, 2—3 mm. long,

often confluent and reaching a length of 1 cm. or more, surrounded by the cleft epidermis, pulverulent, yellow-brown: spores ellipsoid or ovate-oblong, echinulate, yellow-brown, then yellowish, $22-42 \times 16-22 \mu$, generally with four equatorial germ-pores.

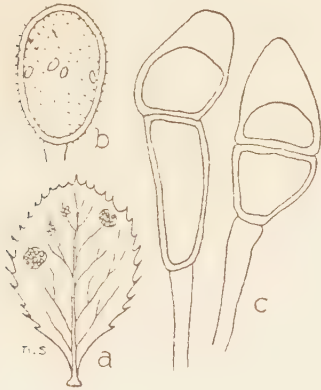


Fig. 193. *P. graminis*. a, æcidia on *Berberis*; b, uredo- and teleutospores on wheat.

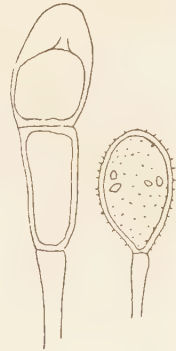


Fig. 194. *P. graminis*. Teleuto- and uredospore on *Aira caespitosa*.

Teleutospores. Sori similar, but forming long lines, soon naked, pulvinate, black; spores oblong-clavate, rounded or attenuated at the summit, much thickened ($6-13 \mu$), slightly constricted, attenuated below, smooth, chestnut-brown, $35-60 \times 12-22 \mu$; pedicels brownish, persistent, thick, as much as 60μ long; paraphyses always absent.

Æcidia on leaves and fruits of *Berberis vulgaris* and *Mahonia Aquifolium*; uredo- and teleutospores on *Agropyron caninum*, *A. repens*, *Agrostis alba*, *A. canina*, *A. vulgaris*, *Aira caespitosa*, *A. flexuosa*, *Alopecurus pratensis*, *Arrhenatherum elatius*, *Avena fatua*, *A. sativa*, *Brachypodium pinnatum*, *Bromus arvensis*, *B. asper*, *B. erectus*, *B. giganteus*, *B. mollis*, *B. secalinus*, *Dactylis glomerata*, *Festuca Myurus*, *F. ovina*, *F. rubra*, *Holcus lanatus*, *H. mollis*, *Hordeum murinum*, *H. pratense*, *H. vulgare*, *Lolium perenne*, *Milium effusum*, *Molinia caerulea*, *Phalaris canariensis*, *Poa compressa*, *P. nemoralis*, *P. pratensis*, *P.*

trivialis, *Secale Cereale*, *Trisetum flavescens*, *Triticum vulgare*. These are the British grasses among those recorded by Sydow: the teleutospores have not been found, and probably do not occur, on all these in this country. (Figs. 193, 194.)

This is the famous "rust" (uredo-) or "mildew" (teleutospores) of corn about which so much has been written. But all the earlier observers confused together the various rusts of Cereals of which a number are now distinguished. *P. graminis* is known as the "Black Rust," on account of the dark colour of the teleuto-sori; these are very distinctive, forming narrow black lines, $\frac{1}{2}$ —1 cm. long, chiefly on the sheaths and culms. However abundant this species may have been in the past, it is much less common in many parts of England now than some of the following species. Whether this is due to the general extirpation of wild Barberry bushes or not, is not certain; at any rate they are very uncommon, and the acidium on the cultivated species of *Berberis* and *Mahonia* is rarely met with in England.

The test by which alone the Black Rust can be absolutely distinguished is the power possessed by its basidiospores of producing the characteristic acidia on the Barberry. There is a European but possibly non-British species of *Puccinia* (*P. Arrhenatheri*) which has also the Barberry for its alternate host, on which it produces peculiar "witches'-brooms," the mycelium living perennially in the twigs. This is *Æcidium graveolens* Shuttl., which was formerly wrongly identified with *Æ. magelhaenicum* Berk. from Tierra del Fuego.

The uredo-stage of *P. graminis* can generally be recognised in the field by its sori, which may reach a length of 10–15 mm. and are of a rusty-orange or brownish-ochre colour; they do not become general till the beginning of June. Forms of *P. dispersa* are often mistaken for it.

Microscopically, the uredospores are seen to be longer compared with their breadth (more ellipsoid) than is the case with the other cereal species; the teleutospores, which germinate only after a winter's rest, are longer and have longer pedicels; their sori form much more conspicuous lines and do not remain for long covered by the epidermis. It is the uredo-stage which does the greatest harm to the crops; it is reported to cause much less in the United States, South Africa, Australia and Tasmania, but not much in India.

This species has been divided by Eriksson into six biological races, but they are of a very indefinite character and later researches (see Carleton, '99, p. 52) throw grave doubt upon their reality. At any rate, they are not the same in America as in Europe, though this may be explained by supposing that, since these forms are undergoing evolution at the present moment, the course of this evolution is different in America from what it is in Europe. The existence of these races is, however, important; they show that the wheat cannot necessarily be infected by

the forms which grow upon wild grasses; according to Eriksson this is absolutely true of his "f. sp. *Tritici*," but Carleton found that the uredo from wheat would infect certain wild grasses and that the uredo from some of them, in turn, would infect the wheat. Most of these races can equally infect the Barberry; yet Wheat-Rust abounds in South Africa, Australia and in parts of India, where no species of *Berberis* are indigenous. McAlpine in particular finds *P. graminis* on 27 species of Gramineæ, yet he was unable to infect the Barberry-plants imported from England, even though wheat planted closely around them was covered with the *Puccinia*. He comes to the conclusion that the Wheat-Rust of Australia may be a biological race which has lost the power of producing æcidia owing to the absence of its æcidial host. According to the evidence at present available, this seems also to be the case with other species, e.g. the æcidial host is not known in Australia for *P. Agrostidis*, *P. bromina*, *P. Festucae*, *P. Lolii*, and especially *P. Poarum*. The latter case is the most striking, since the Coltsfoot does not exist in Australia, and the uredospores on *Poa* have been found there all the year round.

The only practicable remedy for this disease is to plant seeds of varieties which have been shown to be immune: a certain progress has already been made by Professor Biffen and others in the production of these, and McAlpine mentions a variety, "Rerraf," which has been found to be rust-resistant in many of the Australian States, though it lost that power when transferred to other countries. In the year 1889, which had a wet and "muggy" spring, the loss due to rust for the whole of Australia was estimated to be between two and three million pounds sterling.

DISTRIBUTION: In every country of the world.

118. ***Puccinia coronata*** Corda.

Æcidium crassum Pers. Syn. Fung. p. 208 p.p. Cooke, Handb. p. 538; Micr. Fung. p. 196 p.p.

Æ. Frangulae Schum. Pl. Säll. ii. 225.

Puccinia coronata Corda, Ic. Fung. i. 6, pl. 2, f. 96. Cooke, Handb. p. 494; Micr. Fung. p. 203, pl. 4, f. 60—2. Plowr. Ured. p. 163 p.p. Sacc. Syll. vii. 623 p.p. Sydow, Monogr. i. 699. Fischer, Ured. Schweiz, p. 373, f. 270.

Spermogones. Epiphyllous or amongst the æcidia.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, in roundish groups or irregularly scattered, on yellow or purplish spots, producing distortion especially of the petioles, cylindrical, with a white torn revolute margin; spores very delicately verruculose, orange, $16\text{--}25 \times 15\text{--}20 \mu$.

Uredospores. Sori amphigenous, but mostly epiphyllous,

scattered or arranged in rows, rarely confluent, minute, more or less oblong, pulverulent, orange; spores globose to ovate, shortly echinulate, yellow, $16-25 \times 14-20 \mu$, with three or four germ-pores (about ten, Fischer, but ?), and mingled with a few paraphyses.

Teleutospores. Sori hypophyllous, irregularly scattered, rarely confluent, oblong or linear, covered by the epidermis, soon naked, black; spores cuneate, flat at the summit and crowned with about 5-7 obtuse (digitaliform) darker-coloured teeth, hardly or not at all constricted, gradually tapering towards the base, smooth, brown, $35-60 \times 12-22 \mu$; pedicels short, rather thick.

Æcidia on *Rhamnus Frangula*, May and June; uredo- and teleutospores on *Agropyron repens*, *Agrostis alba*, *A. stolonifera*, *A. vulgaris*, *Calamagrostis lanceolata*, *Dactylis glomerata*, *Festuca sylvatica*, *Holcus lanatus*, *H. mollis*, *Phalaris arundinacea* (but not yet recorded on all these grasses in Britain), August-October. Common.

On account of the processes at the summit of the teleutospore this species is called Crown Rust. It was surmised by Plowright that there are two Crown Rusts; these have since been called *P. coronata* and *P. Lolii* (= *P. coronifera*). They are equally widely distributed, but are said to occur on different grasses, with the exception that they are both found on the two species of *Holcus*.

In accordance with custom, they are here kept separate, but aside from the distinction of the hosts they can be separated only by minute differences. When they occur on *Holcus*, therefore, the only test that could absolutely decide the matter would be to await the maturation of the teleutospores, and then try if they would infect *R. Frangula*. The lighter-orange colour of the uredo-pustules, and the character of the germ-pores will, however, distinguish either of them from *P. graminis*, when occurring on the same hosts; in the Crown Rusts, moreover, both kinds of sori are confined almost entirely to the leaves.

The teleuto-sori of *P. coronata* have a less decided tendency to group themselves round the uredo-sori than in *P. Lolii*, and do not remain so long covered by the epidermis, becoming naked early in the autumn. In the uredo-sori, Eriksson says that paraphyses occur in *P. coronata* and hardly at all in *P. Lolii*; but the evidence seems to favour the conclusion, in general, that the presence or absence of paraphyses is a note of little importance. Plowright mentions an interesting fact, confirmed by Pole-Evans, that the Crown Rust, when it occurs on *Dactylis*, is an early summer

species and is accompanied by few uredospores, while that on *Lolium perenne* (*P. Lolii*) occurs only in the autumn with a profuse simultaneous development of uredospores. This agrees with my experience. Nevertheless, I consider that *P. coronata* and *P. Lolii* are merely biological forms of one species. The experiments of Carleton, in the United States, have shown that the distinctions of hosts are quite insufficient to discriminate the two forms; among others he succeeded in infecting a host, stated by Eriksson to be confined to *P. coronata*, with spores from a host belonging to *P. Lolii*.

P. Festucae Plowr. belongs to the same group, but has its æcidium on Honeysuckle. Crown Rusts have been found in Europe on many other species and genera of grasses (Sydow, i. 705), but they cannot, in the absence of cultures, be even temporarily arranged under the two heads. Barclay described a form from Simla (*P. coronata* var. *himalensis*) on *Brachypodium silvaticum* with its æcidium on *Rhamnus dahurica*; this has since been raised by Dietel to a species (*P. himalensis*).

It is a remarkable fact that the only other species of *Puccinia* known, provided with the same processes, are two (*P. Mesnieriana*=*digitata*, and *P. Schweinfurthii*) whose teleutospores occur on *Rhamnus*. A somewhat similar form, but with much longer apical processes, is found on *Lonicera* in Turkestan (*P. longirostris* Kom.). These instances are similar to those of *P. fusca* and *P. Pruni-spinosae* already mentioned and can be explained in the same way; see Grove, New Phytologist, 1913, p. 89.

119. *Puccinia Lolii* Nielsen.

Æcidium crassum Pers.; Cooke, Handb. p. 538; Micr. Fung. p. 196 p.p.
Æ. Cathartici Schum. Pl. Säll. ii. 225.

Puccinia coronata Corda; Cooke, Handb. p. 494; Micr. Fung. p. 203 p.p. Plowr. Ured. p. 163 p.p. Sacc. Syll. vii. 623 p.p.

P. Lolii Niels. Ug. für Landmaend. i. 549 (1875). Sydow, Monogr. i. 704. McAlpine, Rusts of Australia, p. 123 and many figures.

P. coronifera Kleb. Zeitsch. f. Pflanzenkr. iv. 132 (1894). Fischer, Ured. Schweiz, p. 375, f. 271.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, seated on yellow or purplish spots, scattered or arranged in groups, producing distortion of the parts, cylindrical, with a whitish torn revolute margin; spores very delicately verruculose, orange, $16-25 \times 12-20 \mu$.

Uredospores. Sori amphigenous, scattered or in large patches, forming blister-like swellings, minute, sometimes confluent, lanceolate or more or less oblong, pulverulent, orange; spores globose to obovate, echinulate, yellow, $18-27 \times 16-24 \mu$,

with three or four inconspicuous germ-pores: paraphyses very few or wanting.

Teleutospores. Sori hypophyllous, sometimes arranged in circles round the uredo-sori, rarely scattered, occasionally con-

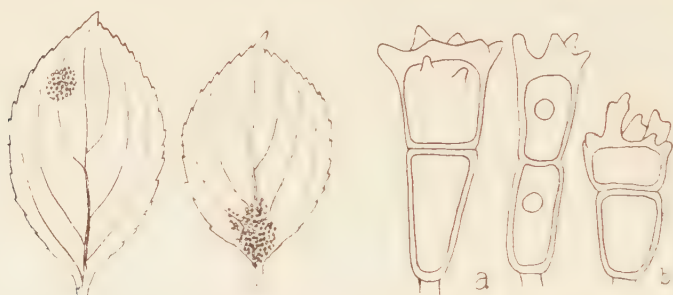


Fig. 195. *P. Lolii*. *Æcidia* on leaves of *R. catharticus*; Teleutospores, *a*, on *Lolium*, *b*, on *Arrhenatherum*.

fluent, oblong or linear, $\frac{1}{2}$ —1 mm. long, nearly always covered by the epidermis, black; spores as in *P. coronata*, but very irregular; mesospores also occur.

Æcidia on *Rhamnus catharticus*, May and June; uredo- and teleutospores on *Alopecurus pratensis*, *Arrhenatherum elatius*, *Avena fatua*, *A. pratensis*, *A. sativa*, *Festuca elatior*, *Glyceria aquatica*, *Holcus lanatus*, *H. mollis*, *Lolium perenne*; not yet recorded on all these species of grass in Britain. (Fig. 195.)

The Crown Rust of the Oat is most commonly found on Rye-grass, frequently also on *Arrhenatherum* and *Holcus*, and also on cultivated Oat which alone of the cereals it attacks, doing considerable damage. The teleutospores can be found on *Arrhenatherum* from the middle of August onwards and, as Plowright remarked, are "accompanied by a profuse development of uredospores"—so profuse, indeed, as to attract the notice of even non-botanical eyes. The uredo-sori form more blister-like swellings and the teleuto-sori remain longer covered by the epidermis than is the case in *P. coronata*. The uredospores are much brighter in colour than those of *P. graminis*.

This species has been divided by Eriksson into a varying number of biological races, of which *P. Lolii Avenae* is the most important; see p. 68. It is found in Australia on Oat and Rye-grass (introduced with seed!) although no species of *Rhamnus* is indigenous there (McAlpine).

DISTRIBUTION: Europe, Asia, North America, Australia.

120. **Puccinia Festucae** Plowr.

Æcidium Periclymeni Schum. Enum. Pl. Säll. ii. 225. Cooke, Micr. Fung. p. 196. Plowr. Ured. p. 264.

Æ. crassum var. *Periclymeni* Cooke, Handb. p. 539.

Puccinia Festucae Plowr. Gard. Chron. 1890, ii. 42, 139, and 1891, i. 460; Grevillea, xxi. 109. Sacc. Syll. xi. 194. Sydow, Monogr. i. 752. Fischer, Ured. Schweiz, p. 377, f. 272. McAlpine, Rusts of Australia, p. 119, f. 13.

Spermogones. In small clusters, honey-coloured.

Æcidiospores. *Æcidia* hypophyllous, on round yellow or brownish spots, in roundish clusters 2—5 mm. diam., shortly cylindrical, whitish-yellow, with recurved irregularly torn margin; spores delicately verruculose, orange, 16—27 μ .

Uredospores. Sori epiphyllous, scattered, minute, oblong, yellow; spores globose to ellipsoid, echinulate, yellow-brown, 22—30 μ , without paraphyses.

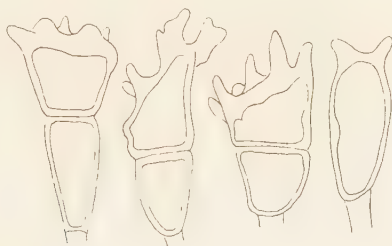


Fig. 196. *P. Festucae.* Teleutospores and mesospore.

Teleutospores. Sori hypophyllous, minute, scattered, oblong or sublinear, black-brown; spores clavate-oblong, crowned at the summit, with four to six curved and sometimes bifid processes, gently constricted, attenuated downwards, smooth, pale-brown, 40—60 $\times$ 15—23 μ ; pedicels brown, persistent, 15—25 μ long; a few mesospores intermixed.

Æcidia on leaves of *Lonicera Periclymenum*, June—August, not uncommon; uredo- and teleutospores on *Festuca duriuscula*, *F. ovina*, August—October, not common or at least rarely observed. (Fig. 196.)

It was Plowright who first, in 1890 (after twenty-eight unsuccessful trials), proved that the well-known æcidium on *Lonicera* was connected

with a Crown Rust on *Festuca*; Klebahn and Fischer have since repeatedly confirmed his results. Fischer records *P. Festucae* for *Festuca rubra* and its var. *fallax*, and he connects it with an *æcidium* on *Lonicera coerulea* and *L. nigra*. He states that the uredospores have about six germ-pores; that the teleuto-sori are situated in the groove of the upper side of the leaf, at first covered by the epidermis which at length opens by a slit; also that the teleutospores have a thick-walled pedicel and are much thickened and occasionally conical at the vertex; mesospores were sometimes found intermixed.

McAlpine found the uredospores with five scattered germ-pores on one face (*i.e.* probably six or more altogether). His specimens were on *Festuca ovina* and *F. rigida*, but in Australia no *æcidium* on *Lonicera* is known. He found very commonly, mixed with the teleutospores, mesospores provided with similar processes at the apex.

DISTRIBUTION: Central and Northern Europe, North America, Australia.

121. *Puccinia glumarum* Er. et Henn.

Uredo glumarum Schmidt, Allg. ökon. Fl. i. 27 (1827).

Trichobasis glumarum Lév.; Cooke, Handb. p. 529; Micr. Fung. p. 223.

Puccinia Rubigo-vera Plowr. Ured. p. 167 p.p.

P. straminis Cooke, Micr. Fung. p. 202 p.p.

P. glumarum Erikss. et Henning, Getreideroste, p. 141. Trans. Brit. Myc. Soc. i. 59. Sydow, Monogr. i. 706. Fischer, Ured. Schweiz, p. 366, f. 265.

Uredospores. Sori amphigenous and on the inflorescence, minute, oblong, as much as 1 mm. long, arranged in long lines, on yellow discoloured spots, not often confluent, lemon-yellow; spores globose to broadly ellipsoid, echinulate, yellow, $25-30 \times 18-26 \mu$; membrane always distinctly colourless.

Teleutospores. Sori hypophyllous or culmicolous, arranged in long fine lines, a few scattered on the inflorescence, oblong, dark-brown or black, covered by the epidermis; spores clavate, rounded, truncate or obliquely conical above, where the exospore may be as much as $4-6$ (or even 10) μ thick, slightly constricted, attenuated below, smooth, brown, $30-70 \times 12-24 \mu$; pedicels very short or almost none; paraphyses brown, numerous, curved, surrounding each little group of teleutospores.

On leaves, culms and glumes of *Agropyron caninum*, *A. repens*, *Brachypodium sylvaticum*, *Bromus mollis* and other species, *Elymus arenarius*, *Hordeum vulgare*, *Secale Cereale*,

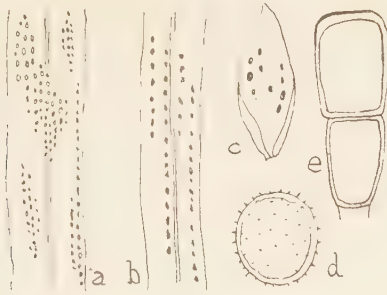


Fig. 197. *P. glumarum*. *a*, uredo-sori and *b*, teleuto-sori, on leaves, nat. size; *c*, teleuto-sori, on glume; *d*, uredospore; *e*, teleutospore.

Triticum vulgare. It is one of the few species that attack the ears, to which it does serious damage. (Fig. 197.)

This is one of two forms originally included under the collective name *P. Rubigo-vera* DC.; they can best be distinguished in the uredo-stage. In the one, *P. glumarum*, the uredo-sori are abundant, clear lemon- or sometimes orange-yellow, and stand in long lines, often occupying half the leaf-blade; in the other, *P. dispersa* and its subordinate forms, they tend towards brownish-orange or even chocolate-brown, and are scattered, rather thinly and without order, over the whole leaf-surface. Eriksson and Henning first proved in 1896 what had been long surmised, that they are quite distinct. *P. glumarum* has no known recidial form, and has been divided into five biological races (see p. 67). It is common in certain districts of England and is called the Spring Rust on account of its early appearance, and Yellow Rust on account of its bright colour, which varies from sulphur- to pale cadmium-yellow. The lines of the uredo-sori may be as much as 7 cm. long, chiefly on the upper face of the leaf; they can be found all the year round on suitable leaves, and are frequently abundant on Wheat as early as the beginning of May. The teleutospores germinate as soon as they are mature; the basidium is yellow until the basidiospores are formed, not colourless as in *P. dispersa*.

On *Hordeum murinum* there is recorded a form, *P. Hordei* Fekl., which has smaller yellow sori, arranged less evidently in lines; this may belong to *P. glumarum* but has not yet been found in Britain. It is probably not identical with *P. simplex* (q. v.).

DISTRIBUTION : Europe, Egypt, North America, Japan.

122. **Puccinia dispersa** (sens. lat.) Er. et Henn.

Trichobasis Rubigo-vera Lév. ; Cooke, Micr. Fung. p. 222, pl. 7, f. 140—2 (?).

Puccinia straminea Cooke, Micr. Fung. p. 202 p.p.

P. Rubigo-vera Plowr. Ured. p. 167 p.p. Sacc. Syll. vii. 624 p.p.

P. dispersa Erikss. et Henning, Getreideroste, p. 210 (1896). Trans. Brit. Myc. Soc. i. 58.

Uredospores. Sori generally epiphyllous or a few hypophyllous, 1—2 mm. long, scattered without order, rarely confluent, oblong or punctiform, rust-coloured or dirty-ochre, becoming paler; spores more or less globose, shortly echinulate, dirty-yellow or dull-orange, $16\text{--}28\mu$; membrane distinctly brownish (pale chocolate-umber) when mature; germ-pores 7—10, scattered over the whole surface.

Teleutospores. Sori hypophyllous or less often on the sheaths, scattered or slightly and irregularly aggregated, rarely in distinct lines, small, oblong, covered by the epidermis, black; spores oblong to clavate, truncate, rounded, or obtusely and obliquely pointed above, slightly thickened, gently constricted, narrowed downwards, smooth, brown, $35\text{--}56 \times 12\text{--}23\mu$; pedicels short; paraphyses numerous, brownish, more or less curved, surrounding the spores.

This is a general description of the forms included under the name Brown Rust, to which the title *P. dispersa* was originally given. The dirty-orange colour of the uredospores, which distinguishes them at a glance from *P. glumarum*, is due to the fact that the membrane of the spores is brownish, not hyaline; the spore contents are orange in colour. The germ-pores are scarcely perceptible in the immature or untreated spore, but they can be seen easily if a spore is squeezed strongly between the cover-glass and the slide, or by choosing a mature and empty spore. In the teleutospores only the upper slightly thickened wall is dark-chestnut, the rest being thin-walled and pale; there is usually also a chestnut-brown band at the apex of the pedicel. The structures called paraphyses here in the teleuto-sori are quite different from those called by the same name in *Melampsora*, etc.; they are erect, coherent, thick-walled, prismatic cells, which surround the teleuto-sori, or in the case of the larger ones divide them into loculi. There are also paraphyses of the ordinary shape, with a brownish membrane, mingled with the uredospores in certain cases, but the occurrence of these seems, so far as is known at present, to be somewhat fortuitous.

Eriksson has divided this species into a number of forms which show certain differences, chiefly biological : they are given in what follows, but it must be understood that they are distinguished almost entirely by their host-plants. They all show the same scattered, brownish-orange uredosori. Some, it is true, have æcidia, others are not known to have them, but this is a difference which time may remove ; also Pole-Evans (1907) has shown that they present minute differences in the mode of germination of their uredospores. Many authors prefer to consider the biological races which follow as distinct species, but if that is done it is a mistake, which entails continual confusion, to retain the name *P. dispersa* for one of them.

DISTRIBUTION : Europe, Asia Minor, North America, and in Australia (probably only introduced).

(1) PUCCINIA SECALINA nov. nom.

Puccinia dispersa (sens. strict.) Erikss. Ann. Sci. Nat. ser. 8, ix. 268, pl. xi, f. 1—6 (1899). Sydow, Monogr. i. 709. Fischer, Ured. Schweiz, p. 357, f. 261. Klebahn, Wirtswechs. Rostp. p. 237.

Æcidium Anchusae Erikss. et Henning, Getreideroste, p. 210.

Æ. Asperifolii Pers. ; Cooke, Handb. p. 541 ; Micr. Fung. p. 197 p.p.

Æcidiospores. *Æcidia* hypophyllous or often on the calyx and fruit, seated on rounded yellowish or reddish-yellow spots, cup-shaped, with an incised revolute margin ; spores verruculose, orange, 20—26 μ .

Æcidia on *Anchusa* (*Lycopsis*) *arvensis*, very rare, Shere, Folkestone, Eltham, etc., August ; uredo- and teleutospores on *Secale Cereale*, May—October. (Fig. 198.)

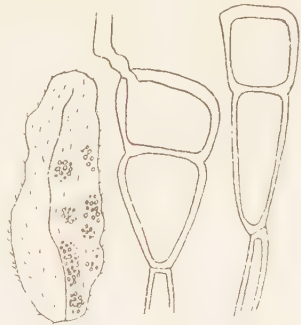


Fig. 198. *P. secalina*. *Æcidia* on leaf of *Lycopsis* ; teleutospores, on neighbouring stems of Rye.

The Brown Rust of Rye in the uredo- and teleuto-stages seems to be confined to that cereal. Eriksson and Klebahn have proved that it can be transferred from species of *Anchusa* to the Rye and *vice-versâ*, but not, they say, to other plants. Plowright's observation (Ured. p. 168) that the æcidium was produced on *Anchusa* by infection from a rusted bundle of wheat straw is discredited by them, but possibly without sufficient reason. The teleutospores are capable of germination as soon as they mature ; hence the æcidium is usually met with in August and September.

(2) PUCCINIA BROMINA Erikss.

Puccinia bromina Erikss. *l.c.* p. 271, pl. xii, f. 12—17. Sydow, Monogr. i. 712. McAlpine, Rusts of Australia, p. 116, pl. C, and fig. 28.

P. Symphyti-Bromorum F. Müll. Beihefte Bot. Centralbl. 1901, x. 201. Klebahn, *l.c.* p. 239. Fischer, Ured. Schweiz, p. 359, f. 262.

P. dispersa Erikss.; Marshall Ward, Ann. Bot. 1902, xvi. 233; Annal. Mycol. 1903, p. 132. Freeman, Ann. Bot. *ibid.* p. 487.

Æcidium Symphyti and *Æ. Pulmonariae* Thüm.

Spermogones. Honey-coloured.

Æcidiospores. *Æcidia* hypophyllous or on the petioles, sometimes even on the calyx, seated on large round or irregular spots which are purplish-brown and surrounded by a yellow zone, cup-shaped, with an incised revolute margin; spores verruculose, orange, 18—27 μ .

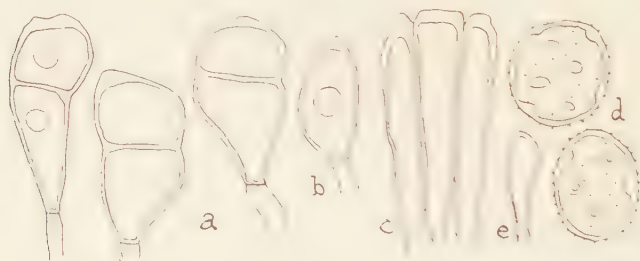


Fig. 199. *P. bromina*. a, teliospores; b, a mesospore; c, paraphyses surrounding the telento-sori; d, uredospores (empty); e, paraphysis in the uredo-sori. On *Bromus sterilis*.

Æcidia on *Symphytum officinale*; uredo- and teliospores on many species of *Bromus*, sometimes even on the inflorescence, teliospores from June onwards. (Fig. 199.)

The teliospores germinate only after the winter's rest; Ward found germinable uredospores even in February and March; it has been proved that an *æcidium* on *Pulmonaria montana* belongs to the same life-cycle. F. Müller, E. S. Freeman, and especially Marshall Ward, have investigated the Brown Rusts of the Bromes, and have discovered a wonderful series of inter-relations among them.

(3) PUCCINIA TRITICINA Erikss.

Puccinia triticina Erikss. *l.c.* p. 270, pl. xi, f. 7—11. Sydow, Monogr. i. 716. Klebahn, *l.c.* p. 245. Fischer, Ured. Schweiz, p. 366.

McAlpine, Rusts of Australia, p. 132, pl. i, f. 3, 6, 10; pl. xl, f. 302; pl. A, f. 1, 2.

On *Triticum vulgare*. June—August. No æcidium is known to belong to it. (Fig. 200.)

The Brown Rust of Wheat has been frequently so abundant in this country in its uredo-stage as to cause great loss. The uredospores can be distinguished from those of *P. graminis*, when both occur upon wheat, by being subglobose, not elongate-ellipsoid, and by the more numerous germ-pores which are scattered instead of forming an equatorial band; also they appear early in spring, before those of *P. graminis*. Sometimes the teleuto-sori occur on the culms, and are then arranged more or less in lines, but they are most common on the underside of the "flag"; their spores germinate only after a winter's rest. Mesospores are not frequent in this species. Klebahn tested the basidiospores of this Rust on forty-two likely species of plants in the hope of discovering an æcidium in its life-cycle, but without any result. The uredospores were found to be capable of surviving the winter by McAlpine in Australia (where it is an introduced species), and by Carleton in the United States south of lat. 40° N.

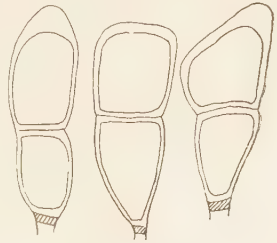


Fig. 200. *P. triticea*.
Teleutospores.

(4) PUCCINIA HOLCINA Erikss.

Puccinia holcina Erikss. *l.c.* p. 274, pl. xiii, f. 22—5. Sydow, Monogr. i. 715. Klebahn, *l.c.* p. 249. Fischer, Ured. Schweiz, p. 365.

On *Holcus lanatus*, *H. mollis*. June—October. Common.

The uredo-stage must be carefully distinguished from that of *P. coronata*, which occurs on the same hosts; the number of germ-pores at once decides the question. The uredo-sori are of a brighter colour than in the other forms of *P. dispersa* and stand upon conspicuous pale spots. The teleutospores are more rarely produced and require to be looked for closely; they resemble those of *P. triticea*, but are mingled with a few mesospores.

(5) PUCCINIA AGROPYRINA Erikss.

Puccinia agropyrina Erikss. *l.c.* p. 273, pl. xii, f. 18—21. Klebahn, *l.c.* p. 249. Sydow, Monogr. i. 712. Fischer, Ured. Schweiz, p. 365.

On *Agropyron caninum*, *A. repens*. August—October. (Fig. 201.)

This is one of the commonest of the Rusts on wild grasses in the autumn, and is easily recognised by the following points: The small scattered dull-orange uredo-sori on the upper leaf-surface; the round faintly echinulate uredospores, which when empty show a pale-chocolate

membrane marked with about nine (7—10) germ-pores, which are each surrounded by a little thickening of the cell-wall, so that they look somewhat like a "bordered pit"; the teleuto-sori mostly on the lower leaf-surface or sheath, black, covered by the epidermis; the teleutospores obconical or with nearly parallel sides, truncate, rounded, or pointed (obtusely and often obliquely) at the apex; the slightly thickened apical wall and a broad band at the base chestnut-brown, but the remainder rather pale; each little group of teleutospores surrounded by a dense wall of brown closely coherent "paraphyses." Oftentimes there are numerous mesospores, especially on the margin of the sorus. The clavate paraphyses which are frequently present in the uredo-sori of other forms of *P. dispersa*



Fig. 201. *P. agropyrina*. *a*, teleutospores; *b*, paraphyses with the same; *c*, plan of paraphyses; *d*, paraphysis with uredospores; *e*, uredospore.

are mostly absent in this; when present they have a thin brownish membrane exactly of the same colour as that of the uredospores. This fungus is as distinctively an autumn parasite as *P. glumarum* is a spring one on the same hosts.

(6) PUCCINIA TRIVETI Erikss.

Puccinia Triveti Erikss. Ann. Sci. Nat. ser. 8, ix. 277, pl. xiii, f. 26—9 (1899). Sydow, Monogr. i. 716. Fischer, Ured. Schweiz, p. 364. Klebahn, *l.c.* p. 249.

On *Trisetum flavescens*. Uncommon: Alvechurch, Hereford, etc. June—October. *P. graminis* occurs on the same host.

(7) PUCCINIA SIMPLEX Er. et Henn.

Puccinia simplex E. et H. Getreideroste, p. 258 (1896). Sydow, Monogr. i. 756. Klebahn, *l.c.* p. 248. Fischer, Ured. Schweiz, p. 368, f. 266. McAlpine, Rusts of Australia, p. 130, pl. i, f. 1, 4, 9 and pl. B, f. 9, 10 (introduced in 1902).

P. Rubigo-vera var. *simplex* Körn. ; Plowr. Ured. p. 168:

On leaves and culms of *Hordeum vulgare* and other species of *Hordeum*. Teleutospores, August, September. (Fig. 202.)

The Dwarf Brown Rust of Barley, distinguished by the fact that it bears few two-celled teleutospores, but very numerous mesospores, which are variable and asymmetrical, slightly thickened at the apex ($4-6\mu$), measuring $25-45 \times 16-24\mu$. It is to be found in the uredo-stage all the year round. The teleutospores germinate in spring; Klebahn tried to infect, with their basidiospores, the same forty-two species which he tested with *P. triticea*, but equally in vain.

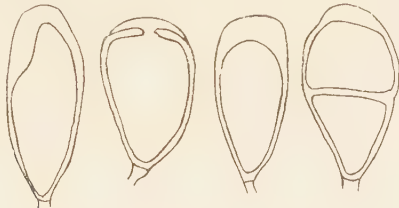


Fig. 202. *P. simplex*. Teleutospores.

P. simplex may be worthy of being regarded as a distinct species; it presents a little more difference from the other forms of *P. dispersa* than they do from one another. The sori of both kinds are amphigenous and more minute and punctiform (except on the culms), and the uredospores are of a brighter yellow. On *Hordeum distichum* I have found sori of *P. simplex* on the leaves, and with them those of *P. graminis* on the culms.

It will be noticed that all the last five races are without any known æcidium; it follows, apparently, that they must maintain themselves by their uredospores, but one might venture to suggest that future, unexpected, discoveries will throw light upon this obscure matter. Eriksson and Klebahn have both proved, by numerous infection experiments, that these races or subspecies of *P. dispersa* are all biologically distinct; with few, and doubtful, exceptions none of them can be transferred from its own to the other hosts.

There are other forms of Brown Rust of which little is known. The æcidium on *Echium vulgare* mentioned by Plowright (Ured. p. 168) may belong to one of these; this plant was one of the forty-two previously mentioned, tested by Klebahn.

I have also some specimens of uredospores on *Aira flexuosa* and *A. caespitosa* sent by Mr T. B. Roe from Scarborough; those

on *A. flexuosa* have no paraphyses, as those on *A. caespitosa* have, but otherwise they are almost identical and are undoubtedly *P. dispersa* (sens. lat.). I find similar spores on *A. caespitosa* round Birmingham, and have a specimen on the same host sent by the late H. T. Soppitt from Saltaire; this latter is the plant referred to in a note to *P. Buryi* (Plowr. Ured. p. 192)—both these have abundant paraphyses with the uredospores. Herr H. Sydow informs me that he considers the presence or absence of these paraphyses to be a character of little importance in *P. dispersa*. It must be remembered that *P. graminis* also grows on *A. caespitosa*, but the uredospores can be easily distinguished by their elliptical shape and three or four subequatorial germ-pores; their membrane is brownish, but without the chocolate tinge of *P. dispersa*.

123. *Puccinia sessilis* Schneid.

Puccinia sessilis Schneid. in Schröt. Brandpilze Schles. p. 19.

P. linearis Rob.; Cooke, Micr. Fung. p. 203.

Æcidiospores. See the descriptions given for the four specialised biological races.

Uredospores. Sori amphigenous, scattered, minute, punctiform or shortly linear, yellow; spores globose to ellipsoid, echinulate, brownish-yellow, $20-28 \times 18-24 \mu$; epispore thin, with about seven germ-pores.



Fig. 203. *P. sessilis*.
Teleutospores and mesospore.

Teleutospores. Sori similar, sometimes confluent, long covered by the epidermis, pulvinate, black; spores oblong or oblong-clavate, rounded or truncate above where they are

darker and slightly thickened ($2-5 \mu$), hardly constricted, somewhat narrowed below, smooth, brown, $35-52 \times 15-22 \mu$; pedicels very short or absent; an occasional mesospore is found.

Æcidia on various species of Monocotyledons; uredo- and teleutospores on *Phalaris* (*Digraphis*) *arundinacea*, uncommon, July—May. (Fig. 203.)

The four following biological races agree exactly in the teleutospores, and these can only be distinguished by their successful use to infect the alternate host; though sometimes the question may presumably be decided by finding one or more of those hosts, in the immediate neighbourhood, affected by the æcidium.

It is evident from the disagreement between various authors that it is impossible to decide to which of the four biological races the name *P. sessilis* Schneid. should be applied: it will be better, therefore, to use it as a collective title, which can be employed in cases where the æcidial host cannot be determined. A fifth race, *P. Schmidiana* Dietel, having its æcidia on *Leucopum*, has not yet been found in Britain.

DISTRIBUTION: Europe and North America.

(1) PUCCINIA DIGRAPHIDIS Soppitt.

Æcidium Convallariæ Schum. Enum. Pl. Säll. ii. 224. Plowr. Ured. p. 264. Soppitt in Gard. Chron. ser. 3, vii. 643.

Puccinia Digraphidis Soppitt in Journ. Bot. 1890, p. 213.

P. intermixta Friend in Gard. Chron. ser. 3, viii. 270 p.p.

P. Paridis Plowr. in Gard. Chron. 1892, p. 137; Journ. Linn. Soc. 1893, p. 43.

P. Smilacæarum-Digraphidis Kleb. Zeitschr. f. Pflanzenk. 1896, p. 261. Fischer, Ured. Schweiz, p. 340, f. 251.

P. sessilis Sydow, Monogr. i. 781.

Spermogones. Epiphyllous or in the midst of the æcidia.

Æcidiospores. Æcidia hypophyllous, loosely clustered on roundish or irregular yellow spots, cup-shaped, with a cut white revolute margin; spores verruculose, yellowish, 19—27 μ .

Æcidia on *Convallaria majalis*, *Paris quadrifolia*. Not common. May and June.

Attempts have been made to subdivide still further the fungi included under this head. *P. Digraphidis* Soppitt, on *Convallaria*, and *P. Paridis* Plowr., on *Paris*, are two of these forms which to their authors appeared under cultivation to be confined to their respective æcidial hosts. But, on the other hand, Klebahn has been able to infect, from one and the same *Puccinia*, both *Convallaria*, *Maianthemum*, *Paris*, and *Polygonatum*; nevertheless his attempts to induce specialisation, by cultivating the fungus year after year on *Polygonatum* alone, had the result that towards the end (while it still grew freely on that genus) it could be transferred only with difficulty or not at all to the other genera. Evidently we have here a case where specialisation is naturally in progress, but has not yet proceeded far enough to effect complete separation.

(2) PUCCINIA ORCHIDEARUM-PHALARIDIS Kleb.

Æcidium Orchidearum Desm. Cat. Plant. omis. p. 26. Cooke, Handb. p. 545; Micr. Fung. p. 200. Plowr. Ured. p. 179.

Puccinia Orchidearum-Phalaridis Kleb. Zeitschr. f. Pflanzenkr. 1899, p. 155. Sydow, Monogr. i. 782. Fischer, Ured. Schweiz, p. 343.

Spermogones. Epiphyllous or in the midst of the groups of æcidia.

Æcidiospores. *Æcidia* hypophyllous, usually in circular clusters on yellow spots, cup-shaped, with a cut white reflexed margin; spores verruculose, yellow, $17-26\mu$, sometimes slightly ellipsoid.

Æcidia on *Orchis latifolia*. Not common. May—July.

It is recorded, on the continent, on several other species of Orchidaceæ. This æcidium must not be confounded with the *Caeoma Orchidis*, which belongs to a Melampsora.



(3) PUCCINIA WINTERIANA Magn.

Æcidium Allii Grev. Flor. Edin. p. 447. Cooke, Handb. p. 545; Micr. Fung. p. 200.

Puccinia sessilis Plowr. Ured. p. 165. Sacc. Syll. vii. 624.

P. Winteriana Magn. in Hedwig. 1894, p. 78. Sydow, Monogr. i. 783.

P. Allii-Phalaridis Kleb. in Pringsh. Jahrb. 1899, p. 399. Fischer, Ured. Schweiz. p. 343.

Spermogones. Epiphyllous or in the midst of the æcidia.

Æcidiospores. *Æcidia* hypophyllous, in circinate clusters on large yellow spots, cup-shaped, with a cut white recurved margin; spores very delicately verruculose, yellowish, $17-26\mu$.

Fig. 204. *P. Winteriana*. Spermogones (sp) and æcidia (aec) on *Allium ursinum*. $\times \frac{1}{2}$.

Æcidia on *Allium ursinum*. Not common. End of May—July. (Fig. 204.)

I have found that in many cases only one cluster is formed (or at most two small ones) on a leaf; this probably indicates a scarcity of active basidiospores. In other localities, however, eight or ten clusters may be found on a single leaf. This æcidium must not be confounded with *Caeoma Alliorum*, which belongs to the Melampsoræ.

(4) PUCCINIA PHALARIDIS Plowr.

Æcidium Ari Desm. Cat. Plant. omis. p. 26. Cooke, Handb. p. 545; Micr. Fung. p. 199.

Puccinia Phalaridis Plowr. Journ. Linn. Soc. 1888, xxxiv. 88; Ured. p. 166. Sydow, Monogr. i. 783.

P. Ari-Phalaridis Kleb. in Pringsh. Jahrb. 1899, p. 399. Fischer, Ured. Schweiz, p. 344, f. 252.

Spermogones. Epiphyllous or a few hypophyllous, dark honey-coloured, in roundish groups.

Æcidiospores. *Æcidia* hypophyllous, in roundish clusters (often surrounding a little group of spermogones), on conspicuous pale-yellow spots, cup-shaped, with a broad cut white revolute margin; spores delicately verruculose, yellow, 15—26 μ .

Æcidia on *Arum maculatum*. Not common. May—July. (Fig. 205.)

The same remark may be made about the occurrence of this as about the preceding form. The three latter races are biologically quite distinct in so far that, in experimental cultures, each of them will produce the æcidium only on that particular genus to which it has become accustomed. This has been abundantly proved by Plowright, Klebahn, Fischer, Dietel and others. But the groups of æcidia are exactly of the same type in each case, and must have had a common origin in the past.



Fig. 205. *P. Phalaridis*.
Æcidia on *Arum maculatum*. $\times \frac{1}{2}$.

124. *Puccinia Anthoxanthi* Fekl.

Puccinia Anthoxanthi Fekl. Symb. Myc. Nachtr. ii. 15. Plowr. Ured. p. 194. Sacc. Syll. vii. 665. Sydow, Monogr. i. 727. Fischer, Ured. Schweiz, p. 261. McAlpine, Rusts of Australia, p. 115, f. 20—1.

Uredospores. Sori amphigenous, on indefinite yellowish spots, scattered or in groups, elliptical or linear, soon naked, minute, rusty-yellow; spores ellipsoid to ovate, delicately echinulate, yellowish, $20-30 \times 15-20 \mu$ (with 2-4 very distinct equatorial germ-pores on one face, McAlpine).

Teleutospores. Sori very inconspicuous, amphigenous, scattered, minute, soon naked, elliptical or linear, blackish-brown; spores elliptical or subpyriform or oblong, usually rounded above and thickened (up to 8μ), gently constricted, rounded or rarely attenuated below, smooth, chestnut-brown, $28-48 \times 16-22 \mu$; pedicels persistent, brownish, up to 45μ long.

On leaves (living or fading) of *Anthoxanthum odoratum*. Very rare; King's Lynn, 1884.

The description is from Sydow, where it is stated that the uredo is frequent in mid-Germany, but the teleutospores are exceedingly rare. Plowright mentions that, mixed with the uredospores, he found a large number of hyaline capitate paraphyses; but Fischer states that the specimen in Sydow's Uredineen (no. 458) has no paraphyses and none are mentioned in the description. In a doubtful specimen on *Anthoxanthum* from Switzerland, however, Fischer found paraphyses. McAlpine also found no paraphyses, but occasional mesospores, and states that the teleutospores are much more uncommon than the uredospores. He found his specimens on sheath and inflorescence of *A. odoratum*, as well as on the leaves. The only British specimens I have seen are those collected at King's Lynn by Plowright in 1884, but it is also recorded for Yorkshire. The suggestion that this is a heterecious species has so far received no confirmation.

DISTRIBUTION: Belgium, Germany, Australia.

125. *Puccinia perplexans* Plowr.

P. perplexans Plowr. Quart. Journ. Micr. Sci. xxv. 164; Ured. p. 179; Hedw. 1886, p. 38; Grevillea, xiii. 53. Sacc. Syll. vii. 632. Sydow, Monogr. i. 719. McAlpine, Rusts of Australia, p. 127, f. 23.

Aecidiospores. Aecidia hypophyllous and on the petioles, clustered on roundish yellow spots, somewhat cylindrical, with a white incised margin; spores faintly verruculose, orange, $18-27 \mu$ diam.

Uredospores. Sori amphigenous, scattered, roundish, oblong or linear, occasionally confluent, minute, yellow-brown; spores globose to ovate, faintly echinulate, yellow, $20-28\ \mu$ diam. (with 4—6 scattered germ-pores on one face, McAlpine).

Teleutospores. Sori amphigenous, scattered, occasionally confluent, minute, generally oblong or linear, about $1-1\frac{1}{2}$ mm. long, always covered by the epidermis, black; spores variable, generally oblong to clavate, rounded, truncate or obliquely attenuated at the apex, slightly thickened ($3\ \mu$) and darker, gently constricted, narrowed below, smooth, brown, $36-57 \times 18-24\ \mu$, with a very short pedicel.

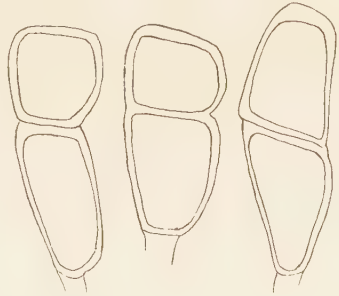


Fig. 206. *P. perplexans*.
Teleutospores.

Æcidia on leaves and petioles of *Ranunculus acris*; uredo- and teleutospores on *Alopecurus pratensis*. Very uncommon. (Fig. 206.)

The connection of the æcidium with the *Puccinia* was first demonstrated by Plowright, and has since been confirmed by Dietel and by Klebahn. All the teleutospores I have seen were full of a very coarsely granular protoplasm. It must not be forgotten that an æcidium on *Ranunculus acris* belongs also to *Uromyces Dactylidis*.

DISTRIBUTION: Holland, Germany and Australia.

126. *Puccinia Magnusiana* Körn.

Æcidium Ranunculacearum DC.; Cooke, Handb. p. 539; Micr. Fung. p. 196 p-p.

Puccinia graminis var. *Arundinis* Cooke, Handb. p. 493; Micr. Fung. p. 202.

P. Magnusiana Körn. in Hedwig, 1876, p. 179. Phill. and Plowr. in Grevillea, xiii. 53. Plowr. Ured. p. 177; Proc. Roy. Soc. Lond. xxxvi. 47; Quart. Journ. Micr. Sci. xxv. 156. Sacc. Syll. vii. 631. Sydow, Monogr. i. 785. Fischer, Ured. Schweiz, p. 241, f. 189. McAlpine, Rusts of Australia, p. 125, f. 18.

Æcidiospores. *Æcidia* hypophyllous in small clusters on yellowish spots, or on the petioles or stems forming elongated groups, cup-shaped, with a cut white margin; spores densely and finely verruculose, yellowish, $15-25\ \mu$.

Uredospores. Sori amphigenous, scattered, rarely confluent, elliptical or oblong, 1—2 mm. long, pulverulent, pale yellowish-brown; spores mostly ovate or ellipsoid, delicately echinulate, pale brownish-yellow, $20-35 \times 12-20\ \mu$; germ-pores indistinct; paraphyses numerous, clavate, hyaline or pale brownish.

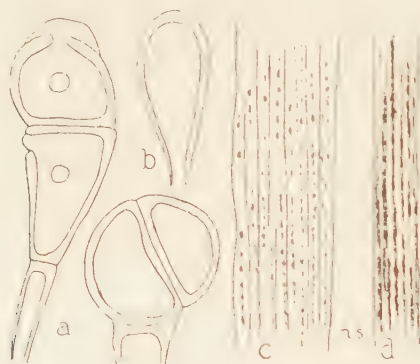


Fig. 207. *P. Magnusiana*. a, Teleutospores (one abnormal); b, paraphysis with uredospores; c, sori on leaf, and d, sori on stem of *Phragmites*.

Teleutospores. Sori amphigenous, very numerous, usually scattered over the whole leaf-surface, oblong or sublinear, minute, 1—2 mm. long, or on the culms and leaf-sheaths forming narrow striae several centimetres long, flat, compact, persistent, blackish; spores oblong or clavate, rounded above or rarely conically attenuate or truncate, with a distinct thickened cap ($5-10\ \mu$), hardly constricted, attenuated downwards, smooth, brown, darker above, $32-55 \times 16-26\ \mu$; pedicels thick, brownish, persistent, as long as or shorter than the spores.

Æcidia on *Ranunculus bulbosus*, *R. repens*, April—June or even July and August; uredo- and teleutospores on *Phragmites communis*, June—April. Not uncommon in suitable localities. (Fig. 207.)

It was Plowright who first proved, by a long series of cultures, that the æcidium of this species is produced only on the two species of *Ranunculus* given above; Klebahn and Fischer have since abundantly confirmed his results. The æcidia belonging to *Uromyces Poae* and *U. Dactylidis* occur on the same hosts and are morphologically quite indistinguishable, but begin to appear earlier in the spring.

P. Magnusiana is distinguished from the two following species by its numerous small teleuto-sori, and the abundant paraphyses mixed with its uredospores; the teleutospores also show hardly any constriction. McAlpine describes mesospores $28-38 \times 13-19 \mu$, and says that the apex of the paraphyses in the Australian specimens is of a dark smoky-brown. This species and *P. Phragmitis* may occur together upon the same leaf.

DISTRIBUTION: Europe, South Africa, Japan, Australia.

127. *Puccinia Phragmitis* Körn.

Æcidium rubellum Gmel. Syst. Nat. ii. 1473. Cooke, Handb. p. 544;

Micr. Fung. p. 199 p.p. Purton, Midl. Flor. iii. 294, pl. 26.

Uredo Phragmitis Schum. Fl. Säll. ii. 231.

Puccinia arundinacea Hedw. in DC. Flor. fr. v. 59. Cooke, Handb. p. 493; Micr. Fung. p. 202.

P. Phragmitis Körn. in Hedwig. 1876, p. 179. Plowr. Ured. p. 175. Sacc. Syll. vii. 630. Sydow, Monogr. i. 787. Fischer, Ured. Schweiz, p. 250, f. 192.

Spermogones. Whitish.

Æcidiospores. Æcidia hypophyllous, on circular red or deep purple spots $\frac{1}{2}-1\frac{1}{2}$ cm. diam., in dense clusters, shortly cylindrical or cup-shaped, with a cut white recurved margin; spores verruculose, nearly hyaline, $16-26 \mu$; spore-mass white.

Uredospores. Sori amphigenous, scattered or subgregarious, elliptical, lanceolate or linear, sometimes confluent, rather large, convex, pulverulent, brown, without paraphyses; spores subglobose or obovate, verruculose rather than



Fig. 208. *P. Phragmitis*. Teleutospores and uredospore; a, sori on leaf of *Phragmites*.

echinulate, brownish, $25-35 \times 16-26 \mu$; contents colourless; epispore rather thick, with four equatorial germ-pores.

Teleutospores. Sori numerous, similar, but larger and thicker, very convex and compact, black; spores oblong, rounded at both ends, thickened ($4-9 \mu$) above, constricted, smooth, deep yellowish-brown, $45-65 \times 16-25 \mu$, sometimes 75μ long; pedicels hyaline or yellowish, thick, persistent, $100-200 \mu$ long.

Æcidia on *Rumex acutus*, *R. crispus*, *R. conglomeratus*, *R. Hydrolapathum*, *R. obtusifolius*, *Rheum officinale*. May and June; uredo- and teleutospores on *Phragmites communis*, July—May, often in the same sori. Not common, except locally. (Fig. 208.)

It was Plowright who first showed that *P. Phragmitis* has its æcidium, not on *Ranunculus*, but on species of *Rumex* and *Rheum* (not, however, on *Rumex Acetosa*). Klebahn and Fischer have confirmed his results, and Arthur has done the same for the North-American forms. It is a remarkable fact, however, that the æcidium had not been previously found in North America until Arthur obtained it artificially by infection of *Rumex crispus* and *R. obtusifolius* with the teleutospores of *P. Phragmitis*. Afterwards it was found in Nebraska on various species of *Rumex* and *Rheum*. It is suggested by Sydow that this species is dispensing with the æcidium, in which case it must winter by means of its uredospores. Even in England the æcidium seems relatively scarce, but it is very conspicuous, and can be found on *Rumex* growing amidst Reeds.

DISTRIBUTION: Europe, South Africa, Japan, North America, Chili.

128. *Puccinia Trailii* Plowr.

Æcidium rubellum Gmel.; Cooke, Handb. p. 544; Mier. Fung. p. 199 p.p.

Puccinia Trailii Plowr. Ured. p. 176. Sacc. Syll. ix. 312. Sydow, Monogr. i. 790. Fischer, Ured. Schweiz, p. 252, f. 193.

Æcidiospores. Similar to those of the last species; but the spots are purple, surrounded by a yellow margin, the æcidia are wider and flatter, and the spores are on the average somewhat larger.

Uredospores. Sori amphigenous, scattered, rather large,

elliptical or linear, reddish-brown, pulverulent, without paraphyses; spores subglobose or ovate, echinulate, brownish, $25-35 \times 20-25 \mu$.

Teleutospores. Sori similar, but larger (2—4 mm.), compact, pulvinate, black; spores oblong, rounded at both ends, with a cap-like thickening ($5-10 \mu$) above, plainly constricted, brown, $50-60 \times 20-23 \mu$; pedicels brownish, thick, persistent, $75-100 \mu$ long.

Æcidia on *Rumex Acetosa*, May and June: uredo- and teleutospores on *Phragmites communis*, from July. Rare. (Fig. 209.)

The results of Plowright's cultures have been confirmed by Klebahn, but at any rate this species is very closely allied to the previous one, and should rather be considered as merely a biological race of it.

DISTRIBUTION: Holland, Germany.

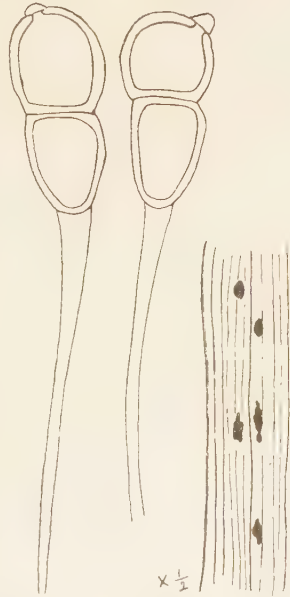


Fig. 209. *P. Trailii*. Teleutospores, and sori on leaf of *Phragmites*.

129. *Puccinia Agrostidis* Plowr.

Æcidium Aquilegiæ Pers.; Plowr. Ured. p. 263.

Æ. Ranunculacearum var. *Aquilegiæ* DC.; Cooke, Handb. p. 539.

P. Agrostidis Plowr. Gard. Chronicle, 1890, ii. 139; Grevillea, xxi. 110. Sacc. Syll. xi. 202. Sydow, Monogr. i. 717. McAlpine, Rusts of Australia, p. 114, f. 27 (?). Fischer, Ured. Schweiz, p. 353, f. 257.

Spermogones. Honey-coloured, on round spots.

Æcidiospores. *Æcidia* on rather large roundish yellow spots which are often thickened and margined with brown, crowded, hypophyllous, shortly cylindrical, with a torn white margin; spores faintly verruculose, orange, $16-30 \times 14-20 \mu$.

Uredospores: Sori amphigenous, on yellow spots, elongated or linear, about 1 mm. long, bright-orange; spores globose to

ovate, yellow, faintly echinulate, $20-25 \times 16-22 \mu$; membrane colourless.

Teleutospores. Sori hypophyllous, minute, covered by the epidermis, oblong or linear, rarely confluent, black; spores somewhat clavate, rounded, truncate or gently narrowed above, slightly thickened (about 5μ), faintly constricted, narrowed below, smooth, brown, darker upwards, $38-48 \times 12-20 \mu$; pedicels very short.

Æcidia on *Aquilegia vulgaris*, Lewes, Sussex; Lake Windermere; Wyre Forest, etc., May, June; uredo- and teleutospores on leaves and sheaths of *Agrostis alba*, *A. vulgaris*, August. Uncommon. The *Puccinia* should be looked for on the grass near the place where the *æcidium* was seen.

The connection between the *æcidium* on *Aquilegia* and the *Puccinia* on *Agrostis* was first demonstrated by Plowright (see Gard. Chron. 1890, ii. 139, and 1891, i. 683); the fact has since been confirmed and extended to *Aquilegia alpina*. McAlpine's species seems to be rather different; he records numerous mesospores, and uredospores with as many as nine germ-pores, circularly arranged, on one face.

DISTRIBUTION: Central and Western Europe, Siberia, India, and (?) Australia.

130. *Puccinia Moliniæ* Tul.

Æcidium Melampyri K. et S. exsicc. no. 165.

Puccinia Moliniæ Tul. Ann. Sci. Nat. ser. 4, ii. 141, pl. ix, f. 9-11.

Cooke, Grevillea, v. 57; Micr. Fung. p. 203. Plowr. Ured. p. 179.

Sacc. Syll. vii. 631. Sydow, Monogr. i. 762. Fischer, Ured.

Schweiz, p. 256, f. 195.

P. nemoralis Juel, Öfers. K. Vet.-Akad. Förh. 1894, p. 506, f. *a-f*.

P. Æcidii-Melampyri Liro, Act. Soc. Faun. et Flor. Fenn. xxix. 55.

[*Æcidiospores.* *Æcidia* hypophyllous, clustered on roundish red or purple spots 3-5 mm. diam., cup-shaped, with a cut white revolute margin; spores very minutely verruculose, yellowish (?), $15-18 \mu$.]

Uredospores. Sori amphigenous, generally hypophyllous, often on brownish or purplish spots, scattered or arranged in lines and confluent, oblong or linear, brown; spores more or less

globose, aculeate, yellow-brown, $20-28 \times 20-24 \mu$; epispore $3-6 \mu$ thick, with three germ-pores.

Teleutospores. Sori similar, often confluent and as much as 8 mm. long, conspicuous, pulvinate, black; spores ellipsoid, rounded at both ends, slightly thickened (up to 5μ) above, hardly constricted, smooth, brown, $32-46 \times 20-30 \mu$; pedicels hyaline or yellowish, curved, persistent, rather thin, very long (as much as 120μ); a few mesospores sometimes intermixed.

[*Æcidia* on *Melampyrum* spp.]; uredo- and teleutospores on *Molinia coerulea*, July—October, Perthshire (Dr B. White). This *æcidium* is not recorded for Britain, and appears to be very rare everywhere. (Fig. 210.)

Plowright, relying upon the experiments of Rostrup, connected the *æcidium* on *Orchis latifolia* with this *Puccinia*, though he himself could not succeed in the infection. Others have similarly failed, and there seems to be little doubt that Rostrup's conclusions were inaccurate. Juel has since then succeeded in showing that an *æcidium*

on *Melampyrum pratense* is part of the life-cycle of a *Puccinia* on *Molinia*, which he named *P. nemoralis*, but of which there is no proof that it is different from *P. Moliniae* Tul. (Juel, *l.c.*). Liro confirms this result and names his species *P. Æcidii-Melampyri* (*l.c.*). The *æcidiospores* are described by Sydow as "yellowish," but Juel describes them as colourless, like those of the allied species *P. Phragmitis* and *P. Trailii*.

Since the *æcidium* on *Melampyrum* has not been found in this country, the British species may turn out, on investigation, to be different from these. For there is a closely allied species or biological race, named by Cruchet (Centralbl. f. Bakter. 2. xiii. 96) *P. Brunellarum-Moliniae*, which has teleutospores very like those of *P. Moliniae* Tul. but its *æcidium* on

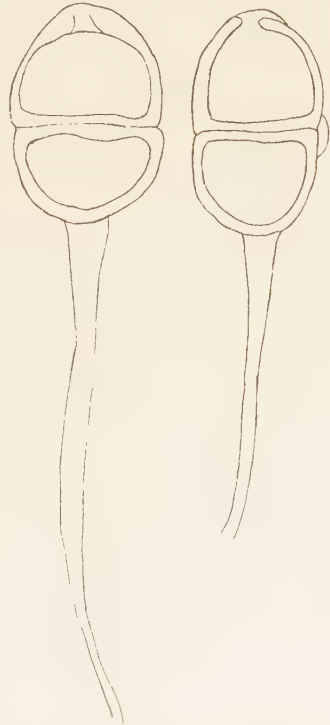


Fig. 210. *P. Moliniae*. Teleutospores, Rannoch (Dr Buchanan White).

Brunella (= *Æcidium Prunellae* Wint.). This was found by Fischer in Switzerland, and the connection of the two hosts was proved by Cruchet. To this, doubtless, belongs the æcidium found on *Prunella vulgaris* by Dr Keith at Forres (Plowr. Ured. p. 264), and Dr Buchanan White's *Puccinia* on *Molinia* may belong there likewise. The apex of the teleutospores in his specimens is, however, much less strongly thickened than in the figures given by Fischer.

DISTRIBUTION: Throughout Europe, except the south.

131. *Puccinia Poarum* Niels.

Æcidium Tussilaginis Gmel. in Linn. Syst. Nat. ii. 1473.

Æ. Compositarum var. *Tussilaginis* Cooke, Handb. p. 542; Micr. Fung. p. 198.

Puccinia Poarum Niels. in Botan. Tidsskr. ii. 26. Phill. et Plow. Grevillea, xiii. 54. Plowr. Ured. p. 168; Grevillea, xi. 52. Sacc. Syll. vii. 625. Sydow, Monogr. i. 795. Fischer, Ured. Schweiz, pp. 361, 556, f. 263. McAlpine, Rusts of Australia, p. 128, f. 22.

Spermogones. Epiphyllous, pale-yellow, often very numerous.

Æcidiospores. *Æcidia* hypophyllous, usually in dense clusters on circular yellowish or reddish thickened spots 1—2 cm. diam., seldom scattered, cup-shaped, with a dentate white revolute margin; spores verruculose, orange, 18—25 × 16—20 μ .

Uredospores. Sori on the leaves, sometimes on the culms, minute, roundish or elliptic, soon naked, yellow; spores globose to ellipsoid, densely and minutely verruculose, yellow, 17—28 × 17—25 μ , with about five scarcely perceptible scattered germ-pores, and intermixed with numerous, hyaline, capitate paraphyses.

Teleutospores. Sori similar, oblong or linear, more or less in short rows, long covered by the epidermis, surrounded by a small pale area, black; spores oblong-clavate, cylindrical, or obconical, variable, rounded, truncate, or rarely conically attenuated above where they are slightly thickened (4—8 μ), hardly or not at all constricted, more or less tapering below, smooth, chestnut-brown, becoming gradually paler downwards

$30-45 \times 16-22 \mu$; pedicels short, brownish, persistent; an occasional mesospore is found.

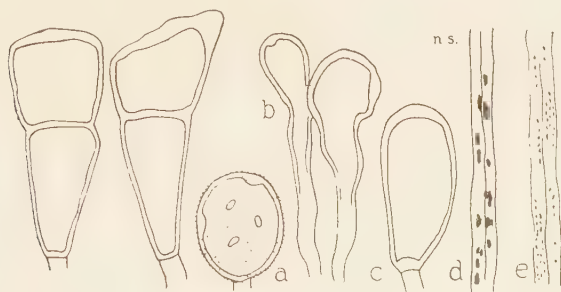


Fig. 211. *P. Poarum*. Teleutospores; a, uredospore on *P. nemoralis*; b, paraphyses with same; c, mesospore; d, teleuto-sori on *P. pratensis*; e, typical teleuto-sori of *Uromyces Poae*, on the same.

Æcidia on *Tussilago Farfara*, about May, June, and August, September, very common; uredo- and teleutospores on *Poa annua*, *P. nemoralis*, *P. pratensis*, *P. trivialis*, about July, August and October—December, common but easily overlooked unless searched for. (Fig. 211.)

First stated by Nielsen, the connection of the two hosts was demonstrated by Plowright and Klebahn. This heterœcious *Puccinia* differs from all others in having two generations in one year. The earlier crop of *æcidia* begins to appear in May, and is followed by the uredo- and teleutospores on the surrounding leaves of *Poa*; these germinate quickly and the second crop of *æcidia* is produced about August, and the second generation of teleutospores may be found on *Poa* from October. The latter germinate in the following spring, but according to Lagerheim the uredospores also, in a favourable climate, can survive the winter. This is certainly true in Australia, where (though the *Puccinia* is an introduced one) the uredospores have been found the whole year round. In that country the Coltsfoot does not exist, and the fungus is carried through the winter by the uredo-stage; in fact, according to McAlpine, it is most common in the winter there. Arthur and Carleton say that the fungus does the same as far north as Nebraska in North America, where the Coltsfoot is only a naturalised plant. Uredospores were found alive in every month of the year at Washington, D.C.

In the Scottish Naturalist ('84, p. 270) this species is recorded for *Poa fluitans*, but there may possibly be some error in this statement. Plowright says that the uredospores are not accompanied by paraphyses,

though others find them habitually. I myself have always found paraphyses (capitate, but not "stiff") in the uredo-sori. McAlpine records three- and even four-celled teleutospores in Australia, and I have found a very few mesospores in the sori.

Perhaps the easiest way to obtain the teleutospores is to search the lower leaves of species of *Poa*, growing round leaves of Coltsfoot, as soon as acidia of the second crop are perceived upon the latter towards the end of July or beginning of August.

DISTRIBUTION: Europe, Japan, North America, Australia.

132. *Puccinia Baryi* Wint.

Epitea Baryi Berk. et Br. Ann. Mag. Nat. Hist. 1854, no. 755.

Lecythea Baryi Berk. ; Cooke, Handb. p. 532 ; Micr. Fung. p. 222.

Puccinia Baryi Wint. Pilz. Deutsch. p. 178. Plowr. Ured. p. 191.

Sacc. Syll. vii. 660. Sydow, Monogr. i. 737. Fischer, Ured.

Schweiz, p. 369, f. 267.

Uredospores. Sori mostly epiphyllous, on linear brown spots, scattered or in groups, often disposed in long linear series, minute, elongated, reddish-brown; spores globose to obovate, delicately verruculose, yellow, $18-25\mu$; paraphyses numerous, clavate to capitate.



Fig. 212. *P. Baryi*. Teleutospores; *a*, abnormal teleutospore; *b*, paraphysis; *c*, uredospore; all on *B. silvaticum*.

Teleutospores. Sori similar, but long covered by the epidermis, blackish-brown; spores very irregular, ellipsoid or sub-clavate or pyriform, obtuse or truncate and slightly thickened and undulated above, hardly constricted, somewhat attenuated below, smooth, clear-brown, darker above, $25-40 \times 15-25\mu$; pedicels none or very short, brownish, darker at base of spore where the transverse wall is much thickened.

On leaves (living or fading) of *Brachypodium pinnatum*, *B. silvaticum*. Not uncommon. July—November, teleutospores not before September. (Fig. 212.)

Both Plowright and Fischer mention that, mixed with the uredospores, are numerous hyaline capitate paraphyses; Sydow's Monographia omits all mention of these. The specimens which I have seen show them always in great numbers.

Often the pedicel of the teleutospores is almost non-existent, and the basal cell-wall is strongly thickened. The upper margin of the teleutospore is often undulated; occasionally one is met with having three cells. An æcidium, though often suggested, has not yet been discovered for this species.

DISTRIBUTION: Central and North-Western Europe.

133. *Puccinia Agropyri* Ell. et Ev.

Æcidium Clematidis DC. Flor. fr. ii. 243. Plowr. Ured. p. 265.

Æ. Ranunculacearum var. *Clematidis* Cooke, Handb. p. 539.

Puccinia Agropyri Ell. et Ev. in Journ. Mycol. vii. 131. Sacc. Syll. xi. 201. Sydow, Monogr. i. 823. Fischer, Ured. Schweiz, pp. 350, 555, f. 255. McAlpine, Rusts of Australia, p. 113.

Spermogones. Amphigenous.

Æcidiospores. *Æcidia* hypophyllous and on the petioles and stems, usually on brownish spots, causing considerable distortion, scattered or in clusters of very varied size, shortly cylindrical, with white torn broadly revolute margin; spores verruculose, orange, 18—27 μ .

[*Uredospores.* Sori amphigenous but generally hypophyllous, on irregular yellow spots, scattered, oblong or linear, 1—1½ mm. long, cinnamon; spores more or less globose, delicately echinulate, pallid-yellow, 19—27 μ ; epispore rather thin, with three or four germ-pores.

Teleutospores. Sori epiphyllous, scattered, sometimes confluent, oblong or linear, as much as 3 mm. long, covered always by the lead-coloured epidermis, black; spores cylindric-clavate,



Fig. 213. *P. Agropyri*. Teleutospores and mesospore, on *A. repens*, Pomerania (ex herb. Sydow).

usually truncate above and thickened (up to 6μ), gently constricted, attenuated downwards, smooth, pale-brown, darker at the apex, $40-80 \times 11-22\mu$; pedicels very short, persistent, somewhat hyaline, with a dark-brown band at the apex.]

Æcidia on *Clematis Vitalba*, May—July; [uredo- and teleutospores on species of *Triticum* (*Agropyron*), but not recorded as yet for Britain]. (Fig. 213.)

Diétel first showed, by culture experiments, that the æcidium on *Clematis Vitalba* is connected with a *Puccinia* on *Triticum glaucum*. In Europe the æcidium is frequently observed (probably because of the striking distortions it produces), but the *Puccinia* has been far more rarely noted, being by no means conspicuous in its appearance. According to Sydow, it occurs also on *Triticum junceum* and *T. repens*, on which it may presumably be found in this country, if looked for.

The statement of Rathay, that *Æcidium Clematidis* belongs to a *Melampsora* on Poplar, is now universally discredited. It has been observed on many (nineteen) species of *Clematis*, but it must be noted, as remarked by Sydow, that the genus *Triticum* is also very widely distributed.

According to Fischer, the teleutospores are often accompanied by brown paraphyses, which subdivide the sori into smaller compartments, something like what obtains in *P. dispersa* and *P. persistens*. Other authors have not found the paraphyses, but they are easily overlooked; abnormal three-celled teleutospores are recorded. Probably more than one species has been included under the name. *P. agropyrina* Eriks. is distinctly different.

DISTRIBUTION: Europe, North and South America, Turk-estan, Japan, Australia.

134. *Puccinia persistens* Plowr.

Æcidium Ranunculacearum var. *Thalictri* Cooke, Handb. p. 540.

Puccinia persistens Plowr. Ured. p. 180. Sacc. Syll. ix. 312. Sydow, Monogr. i. 825. Fischer, Ured. Schweiz, pp. 347, 555, f. 254.

Spermogones. Epiphyllous, in little clusters, orange.

Æcidiospores. Æcidia hypophyllous, in clusters on thickened spots which are purple-brown above and yellow with a brownish border below, urn-shaped or subcylindrical, yellow, with a torn white margin; spores minutely verruculose, orange, $14-28\mu$.

Uredospores. Sori minute, roundish or elongated, orange, on yellowish spots; spores more or less globose, minutely echinulate, yellow, $25-30\ \mu$.

Teleutospores. Sori hypophyllous, minute, ovate, oblong or linear, black, long covered by the epidermis; spores clavate-oblong or irregular, rounded, truncate or obliquely attenuate above, slightly thickened ($4-7\ \mu$), more or less constricted, rounded or often tapering below, smooth, brown, $50-60 \times 15-20\ \mu$; pedicels short, hyaline, persistent.

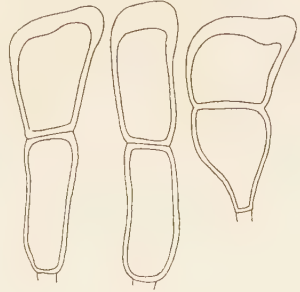


Fig. 214. *P. persistens*.
Teleutospores.

Æcidia on *Thalictrum flavum*, *T. minus*, May—July; uredo- and teleutospores on *Agropyron repens*, from July onwards. (Fig. 214.)

The connection of these spore-forms was ascertained by Plowright and confirmed by Rostrup. The æcidia on various other species of *Thalictrum* may belong to the same Puccinia or to Puccinias on *Agropyron caninum*, *Arrhenatherum elatius* or even on species of *Poa*. There is abundant scope here for further investigation. According to Fischer the teleuto-sori are subdivided into compartments by groups of paraphyses, in the same way as in *P. Agropyri*. In fact the three species, *P. persistens*, *P. Agropyri*, and *P. Actaeae-Agropyri* Fischer, form a natural group which should be regarded rather as biological races of one species, having their teleutospores on *Triticum* (*Agropyron*) and their æcidia on *Thalictrum*, *Clematis* and *Actaea* respectively; the latter (*P. Actaeae-Agropyri*) has not yet been found in Britain.

DISTRIBUTION: Europe, Siberia, Japan, Himalaya, North America.

The evidence for considering the three following species as British is not yet sufficient:—

135. **Puccinia Phlei-pratensis** Erikss. et Henn.

Puccinia Phlei-pratensis Erikss. et Henn., in Zeitschr. für Pflanzenkr. 1894, p. 140; Getreideroste, pl. 5, f. 55—6. Sacc. Syll. xi. 204. Sydow, Monogr. i. 784. Fischer, Ured. Schweiz, p. 260.

Uredospores. Sori on the leaves or most often on the culms on the latter and on the sheaths confluent in long lines (as much as 3 cm. long) and splitting the epidermis, on the leaves more often scattered, minute and oblong, 1—2 mm. long, pulverulent, dark yellowish-brown; spores ellipsoid to oblong or even somewhat pear-shaped, aculeate, dirty-yellow, $18-30 \times 15-20 \mu$.

Teleutospores. Sori similar, but chiefly on the culms, black-brown; spores clavate, rounded or conically attenuate above, thickened (up to 8μ), constricted, attenuated below, smooth, brown, $38-52 \times 14-20 \mu$; pedicels brownish, persistent, rather thick, as much as 60μ long.

On leaves and culms of *Phleum pratense* (and *P. nodosum*); also on *Festuca elatior*.

This was separated by the authors from *P. graminis* on the ground that it will not infect *Berberis*; Eriksson has shown that it will feebly infect *Phleum Michelii*, *Secale cereale*, and *Avena sativa*, but not *Triticum vulgare*, *Hordeum vulgare* or *Poa pratensis*. It chiefly occurs in the uredo-stage, and winters thereby or by its mycelium; in many localities the teleutospores are not formed at all. This may be one of the cases where the aecidium has been dropped completely from the life-cycle. I have not seen a British specimen, but it is extremely likely to occur here.

DISTRIBUTION: Germany, Austria, Denmark, Sweden.

136. **Puccinia Arrhenatheri** Erikss.

Aecidium graveolens Shuttl. apud Cooke, in Bull. Soc. Bot. Fr. 1877, xxiv. 315. Sacc. Syll. vii. 778.

Puccinia perplexans Plowr. f. *Arrhenatheri* Kleb. in Abhandl. Natur. Ver. Bremen, 1892, p. 366.

P. Arrhenatheri Erikss. in Cohn's Beiträge zur Biologie d. Pflanz. 1898, viii. 1. Sydow, Monogr. i. 729. Fischer, Ured. Schweiz, p. 345.

[*Spermogones.* Very numerous, minute, covering a great part of the leaf or the whole leaf uniformly.

Aecidiospores. Aecidia, hypophyllous, sometimes even on the flowers, deforming the affected branches, generally distributed densely and evenly over the whole leaf, between cylindrical and cup-shaped, with a torn whitish revolute margin;

spores subglobose or ellipsoid, verruculose, yellowish, $19-32 \times 16-24 \mu$.]

Uredospores. Sori epiphyllous, very rarely hypophyllous, on minute yellow spots, elliptical or oblong, minute, pale rust-coloured; spores globose to ovate, echinulate, yellowish, $19-30 \times 19-26 \mu$, with numerous germ-pores, and mixed with numerous capitate paraphyses which are $10-14 \mu$ broad and as much as 80μ long.

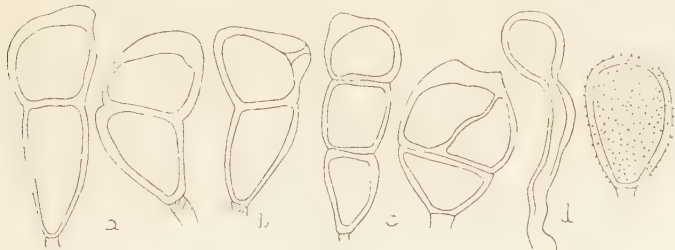


Fig. 215. *P. Arrhenatheri*. a, teleutospores on *Arrhenatherum*, from Hampton-in-Arden; b, another, and c, two abnormal ones, from Lichfield; d, a paraphysis and uredospore from the latter.

Teleutospores. Sori hypophyllous, scattered, minute, punctiform or shortly linear, covered by the epidermis, black; spores ellipsoid-oblong or oblong-clavate, rounded, truncate or rarely gently attenuated above where they are thickened ($5-10 \mu$) and darker, hardly or not at all constricted, generally attenuated downwards, smooth, pale-brown, $30-45 \times 18-24 \mu$, mixed with brownish paraphyses; pedicels short, brownish.

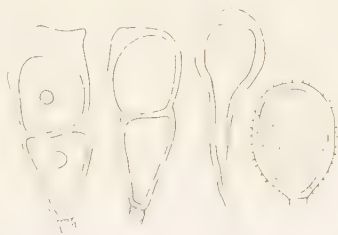


Fig. 216. *P. Arrhenatheri*. Teleutospores, paraphysis and uredospore, on *Arrhenatherum*, Silesia (ex herb. Sydow).

[Æcidia on leaves and flowers of *Berberis vulgaris*;] uredo- and teleutospores on *Arrhenatherum elatius*. (Figs. 215, 216.)

This species produces on the *Berberis* its characteristic witches'-brooms, composed of many upright branches; it was at first mistakenly identified with *Æ. Mughthaenicum* Berk. The æcidium has not been seen in Britain,

but I have found on *Arrhenatherum* on many occasions teleutospores and uredospores which seem to be identical with those of this species, though the former are, in my specimens, often irregularly three- or four-celled.

DISTRIBUTION: Central and Northern Europe, Turkestan.

137. *Puccinia paliformis* Fekl.

Puccinia paliformis Fekl. Symb. Myc. p. 59, pl. ii. f. 17. Plowr. Ured. p. 203. Sacc. Syll. vii. 731. Sydow, Monogr. i. 759, f. 534. Fischer, Ured. Schweiz, p. 264, f. 200.

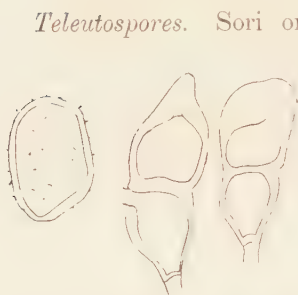


Fig. 217. *P. paliformis*(?). Uredospore and teleutospores, from the specimens collected by Trail.

Teleutospores. Sori on the leaves and culms, scattered, minute, roundish or oblong, up to 1 mm. long, pulvinate, surrounded by the cleft epidermis, black-brown; spores clavate, usually truncate above, more rarely rounded or conically attenuate, much thickened ($10-16\ \mu$), hardly constricted, tapering downwards, smooth, pale-brown, $40-56 \times 10-22\ \mu$; pedicels hyaline, persistent, about as long as the spore.

On *Koeleria cristata*. Very rare. September and October, near Aberdeen (Prof. Trail). (Fig. 217.)

There is much doubt about this fungus; it was suspected by Winter, on account of the likeness of its teleutospores to those of *P. Caricis*, that the original specimens on which the species was founded grew not on *Koeleria*, but on *Carex*. It seems to have been recorded only twice, once by Morthier in the Jura, in spring on old leaves of the previous year, and once as above. The three figures quoted in the synonymy agree fairly well, but appear to have been all taken from the same material, viz. that gathered by Morthier, which according to Sydow may well be *Koeleria* and not *Carex*. I have examined the specimens, preserved in Herb. Kew, gathered by Prof. Trail; they are undoubtedly *Koeleria*, they have split sheaths and, though not in flower, agree perfectly with specimens of *Koeleria cristata* from the Highlands, in the same herbarium. But they bear uredospores in slightly swollen epiphyllous yellow patches, sunken in the leaf (these are mentioned by Prof. Trail in the Scottish Naturalist, 1883, p. 85); therefore the fungus cannot be *P. paliformis* as described by Fuckel, but is probably *P. longissima*, Schröt. I found the uredospores oval or obovate, pale brownish-yellow, sparsely echinulate, $23-24 \times 17-18\ \mu$.

It should be noted that there is an æcidium belonging to *P. longissima*, on species of *Sedum*, formerly called by mistake *Endophyllum Sedi*. This has been found on *S. acre*, and according to Mayor (Annal. Mycol. 1911, ix. 341) on *S. reflexum*, but not, so far as I know, as yet in Britain. Further search in the Highlands will no doubt readily decide which of the two species occurs there.

TRIPHAGMIUM Link.

Autœcious.

Spermogones subcuticular, flattish, without ostiolar filaments. Cæomata indefinite, large, without paraphyses; uredosori small, definite, encircled by paraphyses; spores in both borne singly on pedicels: pores not evident. Teleuto-sori more or less definite; spores coloured, radiately 3-celled, more or less verrucose, with one pore in each cell, equidistant from the septa, i.e. apical.

It is most likely that the foreign species, usually classed with ours on account of the form of the teleutospores, are not closely allied. Spores of this particular shape are met with, abnormally, in other genera, as in several species of *Puccinia*, even in *Puccinia graminis*. Neither is this genus closely allied to *Phragmidium*; the teleutospores have no gelatinous outer coat, and the germ-pores are differently placed.

Tripthragmium Ulmariae Wint.

Uredo Ulmariae Schum. Enum. Pl. Säll. ii. 227.

Uromyces Ulmariae Lév.; Cooke, Micr. Fung. p. 212, pl. 7, f. 147—8.

Tripthragmium Ulmariae Wint. Pilze, p. 225. Cooke, Handb. p. 492;

Micr. Fung. p. 202, pl. 3, f. 47—9. Plowr. Ured. p. 218, pl. 4, f. 6.

Sacc. Syll. vii. 768. Fischer, Ured. Schweiz, p. 423, f. 293.

Arthur, N. Amer. Fl. vii. 178. Sydow, Monogr. iii. 171.

T. Filipendulae Pass. Nuov. Giorn. Bot. Ital. vii. 255. Cooke, Grevillea, xi. 15. Plowr. Ured. p. 219. Masee, in Grevillea, xxi. 115. Fischer, Ured. Schweiz, p. 425, f. 294. Sacc. Syll. vii. 769. Sydow, Monogr. iii. 174.

Spermogones. On the leaves and petioles, circinate, flat, yellowish.

Uredospores. Sori of two kinds—*primary*, i.e. *cæomata*, amphigenous, large, expanded, bright-orange, mostly on the veins and petioles where they cause distortion, without paraphyses; *secondary*, hypophyllous, small, round, scattered, orange, surrounded by paraphyses; spores brilliant-orange, ellipsoid to obovate, verrucose, $25-28 \times 18-21 \mu$, without evident germ-pores.

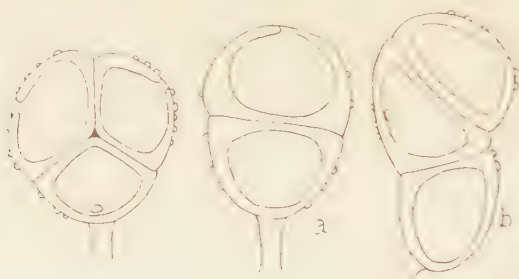


Fig. 218. *T. Ulmariae*. Normal telentospore; a and b, two abnormal ones; on *S. Ulmaria*.

Telentospores. Sori hypophyllous, small, round, brownish-black, persistent, but pulverulent, sometimes arising in the primary uredo-sori; spores subglobose, flattened, chestnut-brown, more or less rough with obtuse warts, $35-49 \mu$; each cell has, at a point opposite to the inner corner, a germ-pore round which the warts are often crowded; pedicels colourless, persistent, variable in length; abnormal spores may have two or four to five cells.

On *Spiraea Ulmaria*, *S. Filipendula*. Very common on the former host. Primary uredospores, May—July; telentospores, August—November. (Fig. 218.)

The primary uredo-sorus may be looked upon as a *cæoma*, i.e. an acidium, and in any case it corresponds to that developmental stage; Klebahn proved (Zeitschr. f. Pflanzenkr. 1907) that it is produced by infection by the basidiospores. Dietel observed that, in elevated situations, the secondary uredo-spore generation on *S. Ulmaria* was almost absent, and the telentospores arose in connection with the primary uredo-sori; this is in agreement with the usual shortening of the life-history that

takes place in arctic and alpine Uredinales. As Plowright remarks, the teleutospores can be found in spring on last year's leaves, and germinate readily when placed in water.

The form on *S. Filipendula*, which is very uncommon in this country, differs from that on *S. Ulmaria* in having the teleutospores usually smooth, and only occasionally provided with a few warts round the germ-pores; but similar spores may be found on both hosts. In both, some of the spores have three super-imposed cells, as in *Phragmidium*, also two cells placed as in *Puccinia* or laterally as in *Diorchidium*. The uredospores on *S. Filipendula* are often pyriform and as much as 35 μ long; it may be a distinct species.

Arthur, who records *T. Ulmariae* in the North American Flora on *Filipendula rubra*, says that it is confined to one locality "of less than a half hectare extent," at Lafayette, Indiana.

DISTRIBUTION : Europe, Siberia, Japan, Indiana.

PHRAGMIDIUM Link.

Autœcious.

Spermogones subcuticular, conical or flattened, without ostiolar filaments. Cæomata indefinite, usually encircled by incurved paraphyses; spores in chains, each with numerous germ-pores. Uredo-sori definite, usually encircled by paraphyses; uredospores borne singly on pedicels, often with paraphyses intermixed, pores numerous, scattered, indistinct. Teleutospores two- to several-celled by transverse septa; wall thick, laminate, usually coarsely verrucose, the middle layer dark and rigid; pores two or more in each cell, placed laterally; pedicels often swollen below; basidiospores globose.

This genus is confined entirely to the family Rosaceæ. There are many species in North America, but with the exception of *P. Potentillae* and those introduced on cultivated roses they are all different from those of Europe. The warts often found on the outer surface of the teleutospores are due to the contraction of the external gelatinous layer, which can be caused to swell up enormously by boiling in lactic acid. This

character, as well as the rigid middle lamina and the position of the germ-pores, distinguishes the genus from all the neighbouring ones.

1. *Phragmidium Fragariastris* Schröt.

Puccinia Fragariastris DC. Flor. fr. vi. 55.

Phragmidium obtusum Link, Sp. Pl. ii. 84 p.p. Cooke, Handb. p. 491; Micr. Fung. p. 201 (as *obtusatum*).

P. Fragariastris Schröt. Flor. Schles. iii. 351. Plowr. Ured. p. 220. Fischer, Ured. Schweiz, p. 412, f. 287. Sacc. Syll. vii. 742. Sydow, Monogr. iii. 101, f. 45.

Spermogones. In little clusters, honey-coloured.

Æcidiospores. Cæomata mostly hypophyllous or on the veins and petioles, irregular, scattered, often confluent and large, bright-orange, surrounded by clavate paraphyses; spores densely verruculose, orange-yellow, $17-28 \times 14-21 \mu$.



Fig. 219. *Ph. Fragariastris*. Uredo-spore, paraphysis, and teleutospore; a, a teleutospore boiled in lactic acid.

Uredospores. Sori hypophyllous, scattered, roundish, soon naked, surrounded by and mixed with hyaline, thin-walled capitate paraphyses; spores roundish, densely verruculose, orange-yellow, $18-24 \mu$.

Teleutospores. Sori hypophyllous, scattered, minute, roundish, pulverulent, brown; spores cylindrical or rarely somewhat clavate, of 2—5 (mostly four) cells, rounded at both ends, sometimes slightly thickened and paler at the summit but never papillate, faintly constricted, rather pale-brown, $45-70 \times 22-28 \mu$, sometimes with a few delicate warts which are more abundant towards the apex, but generally quite smooth; usually three germ-pores to each cell; pedicels colourless, $14-21 \mu$ long.

On *Potentilla Fragariastrum* (= *P. sterilis*), and possibly on other species of the genus, but never on *Fragaria vesca*. March—October. Very common. (Fig. 219.)

The uredospores of this species are distinguished from those of its allies by being densely and rather coarsely verruculose and very similar to the cœoma-spores, from which, in fact, they differ almost solely in being abstricted singly and not in chains. The cœoma-stage is one of the earliest Uredines of spring, showing on the leaves as soon as they are well developed, and extending even to the calyx. The teleutospores are entirely devoid of papilla on the apical cell; the gelatinous outer coat is sometimes almost non-existent, and the spores are but slightly changed by boiling in lactic acid.

DISTRIBUTION: Europe.

2. *Phragmidium Potentillæ* Karst.

Puccinia Potentillæ Pers. Syn. p. 229.

Phragmidium Potentillæ Karst. Fung. fenn. iv. 49. Plowr. Ured. p. 221. Fischer, Ured. Schweiz, p. 410, f. 286. Sacc. Syll. vii. 743. McAlpine, Rusts of Australia, p. 188 (?). Arthur, N. Amer. Fl. p. 174. Sydow, Monogr. iii. 97.

Spermogones. Few, amphigenous, surrounded by the æcidia.

Æcidiospores. Cœomata as in *P. Frugariastri*.



Fig. 220. *Ph. Potentillæ*. *a*, teleutospore $\times 360$; *b*, the same $\times 600$; *c*, the same, boiled in lactic acid for one minute; *d*, a four-celled teleutospore, boiled and distorted by pressure.

Uredospores. Sori hypophyllous, roundish, often confluent, at first covered by the swollen epidermis, surrounded by abundant, clavate, curved paraphyses; spores ellipsoid to obovate, finely echinulate, yellow, $21-24 \times 16-19 \mu$.

Teleutospores. Sori hypophyllous, orbicular, soon naked,

black; spores cylindrical or subclavate, of 3—6 cells (occasionally one or two), rounded or bluntly papillate at the apex, hardly constricted, smooth, brown, $42-80 \times 20-28 \mu$; two or three germ-pores to each cell; pedicels thick, hyaline, persistent, as long as or much longer than the spores ($100-150 \mu$).

On *Potentilla argentea*, *P. verna*, and various cultivated species. April—September. Not common. (Fig. 220.)

This species is more closely allied to *P. Sanguisorbæ* than to *P. Fragariastris*. The finely echinulate uredospores and the papillate teleutospores distinguish it from the latter.

DISTRIBUTION: Europe, Asia Minor, Siberia, Japan, North America, Australia (?).

3. *Phragmidium Sanguisorbæ* Schröt.

Puccinia Sanguisorbæ DC. Flor. fr. vi. 54.

Lecythea Poterii Lévy; Cooke, Micr. Fung. p. 221, pl. 3, f. 31.

Phragmidium Sanguisorbæ Schröt. Flor. Schles. p. 352. Plowr. Ured. p. 221. Fischer, Ured. Schweiz, p. 408, f. 285. Sacc. Syll. vii. 742. Sydow, Monogr. iii. 156.

P. acuminatum Fr.; Cooke, Handb. p. 490; Micr. Fung. p. 201, pl. 3, f. 30, 32.

Spermogones. Amphigenous, flat, clustered.

Æcidiospores. Caemata amphigenous, oblong, circinate round the spermogones, or irregular and swollen on the nerves and petioles; spores verruculose, orange-yellow, $18-21 \mu$; paraphyses curved.

Uredospores. Sori small, scarcely $\frac{1}{4}$ mm., soon naked, surrounded by a circle of clavate, curved paraphyses; spores globose to ovate, echinulate, orange-yellow, $18-24 \mu$.

Teleutospores. Sori punctiform, $\frac{1}{4}-1$ mm., soon naked, black; spores cylindrical-oblong, of 2—5 (mostly four) cells, apex drawn out into a papillate beak, faintly constricted, base rounded, somewhat verruculose, yellowish-brown, $56-$



Fig. 221. *Ph. Sanguisorbæ*. a, teleutospore $\times 360$; b, teleutospore $\times 600$.

70×21 — 24μ ; about three germ-pores to each cell; pedicels hyaline, rather short.

On *Poterium Sanguisorba*. Rather common. Cæomata, April—June; teleutospores, July—November. (Fig. 221.)

DISTRIBUTION: Europe, Algeria, Asia Minor, Turkestan.

4. *Phragmidium disciflorum* James.

Ascophora disciflora Tode, Fung. Meck. sel. i. 16 (*sec.* Sydow).

Coleosporium pingue Lév.; Cooke, Handb. p. 520; Micr. Fung. p. 217.

C. miniatum Pers.; Cooke, Micr. Fung. p. 217.

Lecythea Rosae Lév.; Cooke, Micr. Fung. p. 221, pl. 3, f. 37.

Phragmidium bullatum West.; Cooke, Micr. Fung. p. 202.

P. mucronatum Fr.; Cooke, Handb. p. 490; Micr. Fung. p. 201, pl. 3, f. 38.

P. subcorticium Wint. Pilze, p. 228. Plowr. Ured. p. 224. Fischer, Ured. Schweiz, p. 400, f. 281. Sacc. Syll. vii. 746 p.p. McAlpine, Rusts of Australia, p. 188, f. 229—233, and pl. I, f. 37. Arthur, N. Amer. Flor. vii. 172.

P. disciflorum James, Contr. U.S. Nat. Herb. iii. 276. Sydow, Monogr. iii. 115.

Spermogones. Flat, subcuticular, pale honey-yellow.

Æcidiospores. Cæomata on branches, petioles, leaf-nerves and fruits, often confluent on the branches for long distances, on the leaves mostly roundish, bright-orange; the smaller ones are surrounded by a circle of clavate, thin-walled, colourless paraphyses; spores in short chains, verruculose, orange-yellow, 24 — 28×18 — 21μ .

Uredospores. Sori hypophyllous, very small, scattered, round, soon naked, pale-orange, surrounded by a circle of clavate, curved, colourless paraphyses; spores ellipsoid or ovate, yellow, echinulate, 21 — 28×14 — 20μ , with numerous germ-pores.

Teleutospores. Sori similar, but black; spores ellipsoid to subfusiform-cylindric, of 6—8, rarely five or nine cells, with a pointed papilla which is pale above and darker and scabrous below, not constricted, rounded at base, unevenly warted, red-brown, then blackish-brown, 65 — 120×30 — 45μ ; each cell with two or three germ-pores; pedicels colourless, persistent, about as long as the spore, swollen at the base.

On *Rosa canina*, *R. spinosissima*, and many kinds of cultivated roses. Very common. Cæoma-spores in May and June; teleutospores, August—October. (Fig. 222.)

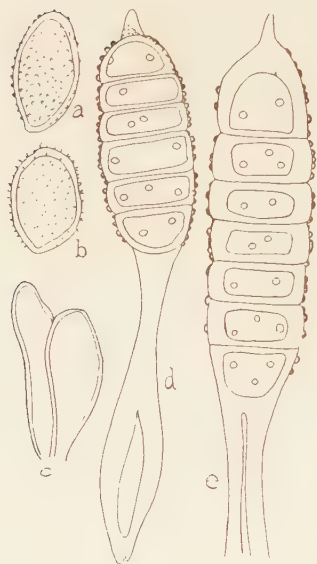


Fig. 222. *Ph. disciflorum*. *a*, aecidiospore, on cultivated Rose; *b*, uredospore, and *c*, paraphyses, on Dog Rose; *d*, a small teleutospore, on the same; *e*, a teleutospore, on Burnet Rose; all $\times 600$.

The teleutospores can germinate in spring, and produce the cæoma (Jacky), but they germinate with difficulty (Müller); the parasite is propagated chiefly by the mycelium of the cæoma-stage, which passes the winter in the branches and in spring bursts out into wide-spreading spore-beds. These attack and destroy the buds; afterwards the uredo- and teleutospores appear on the leaves, with localised mycelium. The infested branches are often swollen and deformed. To keep the disease under control, all teleutospore-bearing leaves and the branches which are permeated by the mycelium should be collected and burnt, and the plant may be sprayed, during the winter, with copper sulphate solution.

It is noteworthy that this fungus occurs in North America only on cultivated roses; the indigenous Rose-

Phragmidia are all different species. It has been introduced, probably by cuttings, also into Australia and other parts of the world.

DISTRIBUTION: Europe, Asia Minor, Persia, Africa, North America, South America, Australia.

5. *Phragmidium fusiforme* Schröter.

Uredo pinguis var. *Rosae-alpinæ* DC. Flor. fr. ii. 235.

P. fusiforme Schröt. Rostpilze Schles. p. 24. Fischer, Ured. Schweiz, p. 404, f. 283. Sacc. Syll. vii. 747. Sydow, Monogr. iii. 121.

Phragmidium Rosae-alpinæ Wint. Pilze, p. 227. Plowr. Ured. p. 226.

Æcidiospores. Sori on the petioles, nerves and fruits, similar to those of *P. disciflorum*, but not so extensive; on the leaves, punctiform and surrounded by hyaline clavate paraphyses; spores echinulate, $17-30 \times 15-20 \mu$.

Uredospores. Sori small, punctiform, yellow: paraphyses like those of the last species; spores roundish, echinulate, yellow, $18-21\ \mu$.

Teleutospores. Sori similar, with similar paraphyses, in little clusters, black; spores cylindrical or fusiform, of $8-13$ cells, attenuated upwards into a pale horny conical process, not constricted, rounded below, verrucose, dark-brown, $80-105 \times 21-24\ \mu$; each cell with two or three germ-pores; pedicels colourless, persistent, sometimes longer than the sporē.

On *Rosa alpina*. Rare; Scotland (introduced). June—October. (Fig. 223.)

This species is very abundant on *R. alpina* in Switzerland. It is distinguished by its numerous, very short, and crowded cells, which are separated by thin partitions.

DISTRIBUTION: Europe.

6. *Phragmidium violaceum* Wint.

Puccinia violacea Schultz, Flor. Starg. p. 459.

Lecythea ruborum Lév.; Cooke, Micr. Fung. p. 221 p.p.

Phragmidium violaceum Wint. Pilze, p. 231.

Plowr. Ured. p. 223. Fischer, Ured.

Schweiz, p. 416, f. 289. Sacc. Syll. vii. 744. Sydow, Monogr. iii. 139.

P. bulbosum Schlecht.; Cooke, Handb. p. 491; Micr. Fung. p. 201, f. 41, 45, 46.

Spermogones. Epiphyllous, in crowded clusters.

Æcidiospores. Cæomata hypophyllous, roundish or elongated, often in circular clusters, on conspicuous spots which are reddish above and surrounded by a violet-red margin, frequently also on the stems; paraphyses few, clavate, straight; spores roundish or ellipsoid, echinulate, orange-yellow, $19-30 \times 17-24\ \mu$.



Fig. 223. *Ph. fusiforme*. Teleutospore.

Uredospores. Sori yellow, roundish, often confluent, pulverulent; spores ellipsoid to ovate, distantly verruculose, yellow, $28-32 \times 21-24 \mu$.

Teleutospores. Sori hypophyllous, large, roundish, thick, pulvinate, black, on conspicuous purple-bordered spots; spores

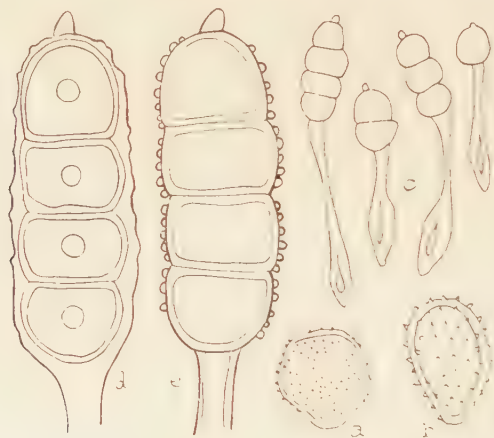


Fig. 224. *Ph. violaceum*. *a*, aëcidiospore; *b*, uredospore; *c*, outlines of various mature teleutospores from the same sorus; *d*, young teleutospore before the middle coat is fully developed, showing the fusion-nucleus in each cell, and the gelatinous outer coat; *e*, mature teleutospore, the pearl-like drops are caused by the shrinking of the outer coat; *c* $\times 200$, the rest $\times 600$.

cylindrical, of 1—5 (mostly four) cells, rounded at both ends, with a short yellowish papilla at the apex, hardly constricted, verrucose, brown, $65-100 \times 30-35 \mu$; two germ-pores to each cell; pedicels long, colourless, swollen at the base.

On *Rubus fruticosus*. Very common, especially near the coast. August—November. (Fig. 224.)

This species is easily distinguished by its large conspicuous red and purple spots, and on microscopical examination by the predominance of four-celled teleutospores. These pass the winter on the leaves, which often remain green on the plant; they germinate with the greatest readiness in April. It is an interesting fact that on some portions of the coast, such as in North Wales, this species predominates, but on other portions, e.g. in parts of Yorkshire, as I was informed by the late Mr. R. H. Philip, its place is largely taken by *P. Rubi*.

DISTRIBUTION: Europe, Egypt.

7. *Phragmidium Rubi* Wint.

Puccinia mucronata var. *Rubi* Pers. Disp. Meth. p. 38.

Phragmidium Rubi Wint. Pilze, p. 230. Plowr. Ured. p. 224. Fischer, Ured. Schweiz, p. 418, f. 290. Sacc. Syll. vii. 745 p.p. Sydow, Monogr. iii. 141.

Spermogones. Epiphyllous, in minute clusters.

Æcidiospores. Caemata hypophyllous, roundish, or on the nerves elongated, often in little groups, surrounded by clavate paraphyses; spores resembling those of *P. violaceum*.

Uredospores. Sori hypophyllous, scattered; spores smaller than those of *P. violaceum*.

Teleutospores. Sori small, on brownish spots, round, scattered, seldom more than $\frac{1}{2}$ mm. diam., black; spores cylindrical, of 4–7 (mostly six) cells, rounded above and mucronate with a colourless acute papilla (5–10 μ long), not constricted, rounded below, brown, beset with numerous little warts, 70–115 $\times$ 28–32 μ , with three (or two) germ-pores to each cell; pedicels hyaline, as long as or longer than the spore, swollen at the base.

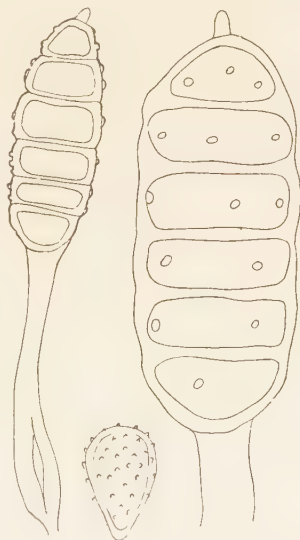


Fig. 225. *Ph. Rubi*. Teleutospore $\times 360$; uredospore $\times 600$; a, teleutospore, boiled in lactic acid for one minute, $\times 600$. On *R. fruticosus*.

On *Rubus fruticosus*, *R. caesius*, *R. saxatilis* (?). Rather less common than *P. violaceum*. July–September. (Fig. 225.)

Distinguished from *P. violaceum* by its smaller teleuto-sori, and by the predominance of six-celled spores; the spots on the leaves are usually much less brilliant in colour. The form on *Rubus saxatilis* may be a distinct species, *P. Rubi-saxatilis* Liro, Ured. Fenn. 1908, p. 421; Sydow, Monogr. iii. 144.

DISTRIBUTION: Europe.

8. **Phragmidium Rubi-Idæi** Karst.

Puccinia Rubi-Idæi DC. Flor. fr. vi. 54.

Lecythea gyrosa Berk. ; Cooke, Micr. Fung. p. 222, pl. 8, f. 162—4.

Phragmidium gracile Cooke, Handb. p. 491 ; Micr. Fung. p. 201, pl. 3, f. 42, 43 ; Grevillea, iii. 171, pl. 45, f. 9.

P. Rubi-Idæi Karst. Myc. Fenn. iv. 52. Plowr. Ured. p. 226. Fischer, Ured. Schweiz, p. 420, f. 291. Sacc. Syll. vii. 748. Sydow, Monogr. iii. 146.

Spermogones. Epiphyllous, in little groups, yellowish.



Fig. 226. *Ph. Rubi-Idæi*. *a*, part of leaf of Raspberry, showing the circular groups of caomata, nat. size ; *b*, a single group, magnified, showing the spermogones in the centre, surrounded by a pulvinate ring of caomata, still partly covered by the epidermis ; *c*, acidiospore and *d*, paraphysis, $\times 600$; *e*, teliospore $\times 300$; *f*, teliospore after boiling in lactic acid ; *g*, single cell of same, showing the three coats, (1) hyaline and gelatinous, (2) dark and rigid, (3) the thin endospore ; *h*, one of the middle coats, detached by pressure, showing the three bordered germ-pores.

Acidiospores. Caomata epiphyllous, small, round, yellow, usually forming a circle round a group of spermogones, surrounded by a dense border of hyaline, clavate, inward-curved,

thin-walled paraphyses; spores ellipsoid or ovate, sparsely echinulate, yellow, $21-24 \times 18 \mu$.

Uredospores. Sori hypophyllous, small, scattered, pale-orange, surrounded by thin-walled clavate paraphyses: spores roundish or ellipsoid, sparsely echinulate, yellow, about $21 \times 18 \mu$; pores obscure.

Teleutospores. Sori similar, but black; spores cylindrical, of 6—10 (mostly 7 or 8) cells, slightly tapering at the apex and papillate, not constricted, rounded below, verrucose, brown, $80-135 \times 28-35 \mu$; three germ-pores to each cell: pedicels very long, thick, colourless, persistent, swollen towards the base.

On *Rubus Idaeus*, and possibly on other species of the genus. Not uncommon. June—October. (Fig. 226.)

Lecythea gyrosa of Berkeley is the caëoma-stage, in which a pulvinate ring of spores is formed round the little group of spermogones, leaving the centre, at first sight, apparently unoccupied. This form is not confined to the early part of the season, but may be found as late as August or September. It is much rarer than the other spore-forms.

Although this *Phragmidium* is not found in America, there is a very similar one, *P. imitans* Arthur, on allied species of *Rubus*, inhabiting the United States and Canada, in which the caëomata are similarly formed.

On the cultivated Raspberry, when this disease is present, it can be prevented from spreading by spraying with potassium sulphide solution or *dilute* Bordeaux mixture. All diseased leaves should be burnt.

DISTRIBUTION: Europe, Siberia, Japan.

KUEHNEOLA Magnus.

Autœcious.

Spermogones subcuticular, somewhat flattened, without ostiolar filaments. Uredo-sori of two kinds: *primary*, i.e. the equivalent of the caëomata, often surrounding the spermogones, without paraphyses; *secondary*, similar, but scattered, sometimes with paraphyses; uredospores borne singly on pedicels, with few and inconspicuous equatorial pores. Teleutospores of

several cells as in *Phragmidium*, but the wall is faintly coloured or colourless, and smooth; pores one in each cell, apical.

This genus is not confined to Rosaceae, being recorded on Malvaceae in America, where also both the British species are found. It is not closely allied to *Phragmidium*: the wall of the teleutospores and the germ-pores are quite different. But I am also of the opinion that the two species included here are not in reality congeneric.

1. *Kuehneola albida* Magnus.

Uredo Mülleri Schröt. Flor. Schles. iii. 375. Plowr. Ured. p. 256.

Chrysomyxa albida Kühn, Bot. Centralbl. xvi. 154 (1883). See also Bull. Soc. Myc. Fr. xvii. 31.

Phragmidium albidum Lagerh. Mitth. Bad. Bot. Ver. 1888, p. 44. Fischer, Ured. Schweiz, p. 415.

Kuehneola albida Magn. Bot. Centralbl. lxxiv. 169 (1898).

K. Uredinis Arthur, N. Amer. Fl. vii. 186 (1912).

Spermogones. Epiphyllous, clustered on small reddish spots.

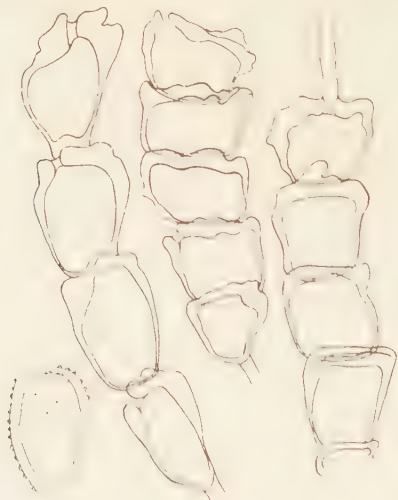


Fig. 227. *K. albida*. Uredospore and teleutospores.

Uredospores. Sori, *primary* epiphyllous, yellow, often in rings surrounding the spermogones, *secondary* hypophyllous, scattered, occasionally on the calyx and stems, smaller, punctiform

and paler, when old whitish; spores globose, obovate or irregularly polygonal, closely verruculose-echinulate, yellow, about $20-26\mu$; pores indistinct (? three or four).

Teleutospores. Sori hypophyllous, singly or in little roundish groups, but never confluent, $\frac{1}{4}-\frac{1}{2}$ mm., pulvinate, yellowish-white; spores cylindrical-clavate, flattened and irregularly coronate at the summit, of 2—13 (mostly 5 or 6) trapezoidal cells which are smooth and colourless, each measuring $17-30 \times 15-25\mu$; the wall of each cell becomes thicker from below upwards, and the upper edge is irregularly undulated; the germ-pore is situated in one of the finger-like projections at the upper edge of each cell; pedicels very short, sometimes wanting; each cell is really a perfectly distinct spore.

On *Rubus fruticosus*. Not rare; Taunton, Hereford, Worcestershire, Woolmer, New Forest, North Wootton, Ayrshire, Ireland, etc. Teleutospores, September—November. (Fig. 227.)

The life-history of this species is imperfectly known. The uredospores may precede the teleutospores, but may also be found simultaneously with them and (presumably the *secondary* uredospores) even in the same sorus. The primary uredospores seem to occur in chains, represent æcidiospores, and probably germinate at once. The teleutospores germinate *in situ* on the leaves as early as the beginning of September. Juel, who experimentally demonstrated the connection of the two spore-forms, suggested that some uredospores survive the winter and germinate in the spring; J. Müller and S. Strelin state the same of the *secondary* uredospores.

This species is said to be found on *Rubus caesius*; it occurs on many species of *Rubus* in North America. The name given by Arthur (*K. Uredinis*) rests upon a (probably true) idea that the teleutospores constitute the fungus named by Link *Oidium Uredinis* and placed among the Hyphomycetes: see Sacc. Syll. iv. 16.

DISTRIBUTION: Europe, North America.

2. *Kuehneola Tormentillæ* Arthur.

Phragmidium Tormentillæ Fekl. Symb. Myc. p. 46. Plowr. Ured. p. 222. Fischer, Ured. Schweiz, p. 414, f. 288. Sacc. Syll. vii. 744. Sydow, Monogr. iii. 105.

P. Potentillæ-canadensis Dietel in Hedwig. Beibl. xlii. 179. Sydow, Monogr. iii. 106, f. 48.

Kuehneola Tormentillæ Arthur, Res. Sci. Congr. Vienn. p. 342 (1904). *K. obtusa* Arthur, N. Amer. Fl. vii. 185 (1912).

Spermogones. Epiphyllous, in little groups.

Uredospores. Sori of two kinds, *primary* epiphyllous, surrounding the spermogones, *secondary* hypophyllous, scattered, small, round, punctiform, orange, surrounded by a few clavate paraphyses; spores spherical to obovate, finely echinulate, reddish-orange, $20-23 \times 14-20 \mu$.



Fig. 228. *K. Tormentillae*.
Teleutospores.

Teleutospores. Sori hypophyllous, similar, but bright-brown; spores cylindrical, fusiform or clavate, of 2-7 (mostly five) cells, often curved, thickened at the apex like many *Pucciniae*, slightly constricted, tapering below, smooth, sienna-brown, $52-140 \times 18-24 \mu$;

epispore thin, with one germ-pore in each cell; contents orange; pedicels varying in length, persistent, not much widened below.

On *Potentilla Tormentilla* (= *P. erecta*) and possibly on other species of the genus. Very rare. September, October. (Fig. 228.)

This species resembles a *Puccinia* in some respects, especially in the thickening of the apex of the teleutospores, and the position of the solitary germ-pore of each cell; the wall of each cell becomes darker upwards, the lower cells being nearly colourless, and the uppermost a pale clear brown, all quite free from any warts or projections. They can germinate in autumn (September) like those of *K. albida*. Dietel says that the uredospores and their mycelium can survive through the winter.

DISTRIBUTION: Europe, North America.

XENODOCHUS Schlecht.

Autecious.

Cæomata large, indefinite, without paraphyses or peridium. Uredospores absent, represented by the secondary smaller cæomata. Teleuto-sori similar, often on the same mycelium; teleutospores of very long chains of cells, not verrucose.

Arthur records and names another species, *X. minor*, on *Sanguisorba latifolia*, from Alaska.

Xenodochus carbonarius Schlecht.

Xenodochus carbonarius Schlecht. in Linnæa, i. 237, pl. 3, f. 3. Cooke, Handb. p. 489; Micr. Fung. p. 201, pl. 3, f. 29. Plowr. Ured. p. 227. Sacc. Syll. vii. 751.

Phragmidium carbonarium Wint. Pilze, p. 227. Fischer, Ured. Schweiz, p. 406, f. 284. Sydow, Monogr. iii. 157, f. 67.

Æcidiospores. Cæomata hypophyllous, on coloured spots, elongated, large, erumpent and pulverulent on the nerves, petioles and stems, roundish and scattered on the leaves, bright orange-red or vermilion; spores roundish to oblong, verruculose, orange, $18-24\mu$, in short chains.

Teleutospores. Sori amphigenous, often confluent with the cæomata, roundish, soon naked, thick, large, pulvinate, black; spores elongated-cylindrical, often curved, of 4—22 cells, rounded at both ends, strongly constricted, smooth, dark-brown, $200-300 \times 24-28\mu$; each cell with two opposite germ-pores at the upper margin, except the uppermost which has one apical germ-pore; pedicels very short, persistent. The whole chain is surrounded by a distinct subhyaline membrane, which swells up considerably in lactic acid.

On *Sanguisorba officinalis*. Not uncommon. June—October. (Fig. 229.)

The teleutospore-cells of the Burnet Chain Rust mature from above downwards, the upper ones being darkest and the lower ones often colourless. There are no uredospores; perhaps they are represented by secondary æcidiospores. The distinctions of this species from the other Phragmidieæ are quite sufficient to justify its generic separation.

Winter assigns to the cæomata clavate paraphyses which I cannot find.

DISTRIBUTION: Europe, Asia.

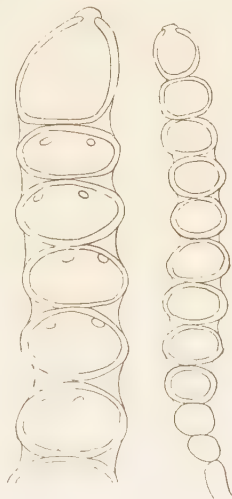


Fig. 229. *X. carbonarius*. Teleutospore $\times 360$; upper part of same, $\times 600$.

GYMNOSPORANGIUM Hedw. fil.

Heterœcious. All the sori subepidermal.

Spermogones spherical, with ostiolar filaments. Æcidia more or less elongated or tubular; peridium membranous, rupturing by lateral slits; spores brown, with numerous evident germ-pores. Teleuto-sori erumpent, naked, variously shaped, gelatinous, expanding when moist; spores with long pedicels, usually two-celled, generally with two pores (1—4) in each cell, mostly near the septa; the cell-wall of the pedicels becomes gelatinised. Germination by an ordinary basidium and roundish basidiospores: these are thrown off with a jerk, at maturity, like the spores of the Hymenomycetes (Coons, 1912).

There are many species of *Gymnosporangium* in America (Kern in N. American Flora gives 32), of which only three occur in Europe, and one or two in Japan. Several of these have three, four, or five-celled teleutospores. The æcidia of the *Gymnosporangia* are on Rosaceæ (except one on Hydrangeæ); the teleutospores are all on Cupressineæ (*Juniperus*, *Cupressus*, *Chamaecyparis*, *Libocedrus*), on which they often form swellings, i.e. galls. But we get also one remarkable exception to this rule in the autœcious species (the only one known) *G. bermudianum*, which produces both its æcidia and its teleuto-sori on Junipers (*J. bermudiana* and other species).

1. **Gymnosporangium clavariæforme** DC.

Tremella clavariæformis Jacq. Collect. ii. 174.

Podisma Juniperi Fr.; Cooke, Handb. p. 510; Micr. Fung. p. 214.

Roestelia lacerata Tul.; Cooke, Handb. p. 534; Micr. Fung. p. 193, pl. 2, f. 22-6.

R. carpophila Bagnis, Flora, lxiii. 317.

Gymnosporangium clavariæforme DC. Flor. fr. ii. 217. Plowr. Ured. p. 233. Fischer, Ured. Schweiz, p. 383, f. 275. Sacc. Syll. vii. 737 p.p. Kern, in North Amer. Fl. vii. 202. Sydow, Monogr. iii. 59, f. 29.

Spermogones. Numerous, amphigenous, but chiefly epiphyllous, in little clusters on red spots, yellow, then dark-brown.

Æcidiospores. *Æcidia* clustered on yellow or orange thickened spots on the leaves, fruits, and stems, cylindrical, up to



Fig. 230. *G. clavariaeforme*. *Æcidia* (*Ræstelia*) on leaf, fruit and branch of Hawthorn (reduced); a, peridium $\times 16$. The fruit and gall on branch are shown as they appear when the peridia are old and the mass looks somewhat like a honey-comb.

$2\frac{1}{2}$ mm. high, fimbriate above, at length lacerate to base, pale-brown; spores verruculose, brownish, about $28-30\mu$; pores $8-10$, scattered.

Teleutospores. Spores collected in long, cylindrical, conical, ribbon-like or tongue-shaped masses about 1 cm. long, which are at first firm, then gelatinous, finally horny when dry, pale-orange, protruding from fusiform swellings of the branches; spores fusiform, varied much in length and breadth, from thick-walled, $50-60 \times 15-21\mu$ to thin-walled, $100-120 \times 10-12\mu$, rounded or attenuated above, hardly constricted, tapering gradually below, smooth, dark yellowish or pale-brown; germ-pores two in each cell; pedicels hyaline, very long.



Fig. 231. *G. clavariaeforme*. Masses of teleutospores on branch of *J. communis* (reduced); teleutospores $\times 600$.

Æcidia on *Crataegus Oxyacantha*, *C. monogyna*, *Pyrus communis*, July—August: teleutospores on *Juniperus communis*, April and May. Rather common. (Figs. 230, 231.)

The teleutospore-mycelium is perennial in the branches of the Juniper; the spores are produced in spring and germinate immediately. The æcidia can be produced on the Hawthorn in two to four weeks or more after infection. Their spores in turn infect young shoots of Juniper, in which the mycelium gives rise to teleutospores in one year (von Tubeuf), or two years (Plowright), and in each succeeding year so long as the branch survives. The mycelium in *Crataegus* is purely local and annual.

The experimental culture of this species has been performed unnumbered times by many mycologists; the æcidia have been produced on several species of *Crataegus* and possibly on the Apple and the Medlar; also (spermogones only in some cases) on *Cydonia*, *Sorbus*, and *Amelanchier*—and the teleutospores on *Juniperus nana* and *J. oxycedrus*, as well as on *J. communis*. This culture is one of the easiest to perform of all that are known among the Uredinales.

The only means of checking this disease on the pomaceous hosts is by the removal of the affected Junipers, if they can be found.

DISTRIBUTION: Europe, Algeria, North America.

2. *Gymnosporangium confusum* Plowr.

Æcidium Mespili DC. Flor. Fr. vi. 98.

Roestelia Cydoniae Thüm. in Sacc. Syll. vii. 834.

Gymnosporangium confusum Plowr. Ured. p. 232, pl. 4, f. 13, 14.

Fischer, Ured. Schweiz, p. 385, f. 276; Zeitschr. f. Pflanzenkr. 1891, i. 193, 260. Sydow, Monogr. iii. 56, f. 27.

Spermogones. Orange-coloured.

Æcidiospores. Æcidia on thickened spots, obconical or cylindrical, opening at the summit which is at length fimbriate, orange above, often surrounded by a reddish or purple line; spores verruculose, pale-brown, 21—24 μ .

Teleutospores. Spore-masses at first pulvinate, dark chocolate-brown, almost black, then irregularly conical, 5—8 mm. long, chestnut-brown, swelling when moist; spores oval to fusiform, smooth, of two kinds, some with hyaline spore-walls and orange contents, tapering above, others with dark-brown thick walls, rounded above, about 30—50 $\times$ 20—25 μ ; germ-pores 2—4; pedicels hyaline, rather long.

Æcidia on leaves, branches and fruits of *Crataegus Oxyacantha*, *C. monogyna*, *Mespilus germanica*, *Cydonia vulgaris*, June—August; teleutospores on *Juniperus Sabina*, April and May; uncommon. (Fig. 232.)

The course of the life history of this species is identical with that of the preceding. It is distinguished by its shorter and broader teleutospores, which resemble those of *G. Sabinae*, but the *æcidia* are quite different from those of that species and resemble those of *G. clavariaeforme*. The *æcidia* of *G. confusum* are reported also doubtfully on *Pyrus communis* and *Cotoneaster integerrimus*. The cells of the peridium have their side-walls marked with elongated obliquely placed ridges, while those of *G. clavariaeforme* have them coarsely warted. This description is taken from Fischer and Plowright, both of whom give long accounts of its peculiarities. In all Plowright's specimens of *G. confusum* (produced artificially on Hawthorn, Quince, Medlar) the peridia were smaller, shorter, less deeply torn, and rather more inflated than those of *G. clavariaeforme*, i.e. of the typical *R. lacerata*.

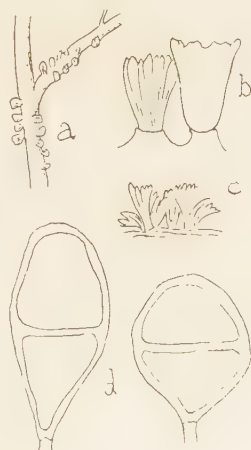


Fig. 232. *G. confusum*. a, cluster of *æcidia* on Hawthorn twig, nat. size; b, two peridia of same $\times 10$; c, cluster of *æcidia* on Quince leaf, $\times 5$; d, two teleutospores on *J. Sabina* $\times 600$. All from cultures by Plowright.

DISTRIBUTION: Europe, Northern Persia.

3. *Gymnosporangium Juniperi* Link.

Tremella juniperina L. Sp. Pl. p. 1625.

Roestelia cornuta Tul.; Cooke, Handb. p. 534, f. 218; Micr. Fung. p. 193, pl. 2, f. 18, 19.

Gymnosporangium Juniperi Link, Obs. i. 7. Cooke, Handb. p. 509, f. 203; Micr. Fung. p. 214. Sydow, Monogr. iii. 27, f. 11.

G. juniperinum Fr. Syst. Myc. iii. 506. Plowr. Ured. p. 235. Fischer, Ured. Schweiz, p. 391, f. 278. Sacc. Syll. vii. 738 p.p.

G. cornutum Arthur, Mycologia, i. 240. Kern, N. Amer. Fl. vii. 198.

Spermogones. Epiphyllous, subepidermal, in roundish crowded groups, yellowish, at length black.

Æcidiospores. *Æcidia* hypophyllous, in irregular or circular groups, horn-shaped, conical, curved, $\frac{1}{2}$ mm. wide, 2 mm. long, at length open and fimbriate above, yellowish-brown, on round spots which are brownish below, and bright-orange or red on the upper side; spores finely verruculose, brown, $21-28 \times 19-24 \mu$; germ-pores 8-10, scattered.



Fig. 233. *G. Juniperi*. Groups of acidia on leaflet of Mountain Ash $\times 1\frac{1}{2}$; a, an unopened peridium $\times 5$.

Teleutospores. Spore-masses on young twigs and occasionally on leaves, more or less globose, 1-3 mm. across,

at first chocolate-brown, then orange, soft, gelatinous; spores obtusely fusiform, of two kinds, *first* thick-walled and brown, *second* thin-walled and yellowish, $31-52 \times 21-30 \mu$ (Dietel), $66-75 \times 17-27 \mu$ (Plowright); germ-pores one or two in each cell; pedicels rather long.

Æcidia on *Pyrus Aucuparia*, July-October; teleutospores on *Juniperus communis*, May and June. Not common; Surrey, etc. *Æcidia* very abundant at Blair Athol, August, 1905 (D. Prain). (Fig. 233.)

The teleutospores differ from those of the other European species in the possession of a broad colourless papilla over each germ-pore. Their mycelium causes fusiform swellings of the smaller branches. Brebner infected a leaf of Mountain Ash from the teleutospores and obtained spermogones in eleven days.

DISTRIBUTION: Europe, North America.

4. *Gymnosporangium Sabinæ* Wint.

Tremella Sabinæ Dicks. Pl. Crypt. Brit. i. 14.

Podisoma Sabinæ Fr.: Cooke, Handb. p. 510; Mier. Fung. p. 214.

Roestelia cancellata Reb. Fl. Neom. p. 350. Cooke, Handb. p. 533; Mier. Fung. p. 193, pl. 2, f. 20, 21.

Gymnosporangium Sabinæ Wint. Pilze, p. 232. Plowr. Ured. p. 230, pl. 4, f. 11, 12. Fischer, Ured. Schweiz, p. 394, f. 279. Sacc. Syll. vii. 739. Sydow, Monogr. iii. 51, f. 26.

Spermogones. Epiphyllous, on large yellow or orange spots, very crowded, at length black.

Æcidiospores. *Æcidia* hypophyllous, on the same spots, flask-shaped, 1—2 mm. broad, pale-brown, split to the base into laciniae which remain united at the summit, and at first are joined at intervals by short transverse bands; spores finely verruculose, brown, $28-30\ \mu$ (average).

Teleutospores. Spore-masses on the branches, at first pulvinate, dark-brown, then irregularly conical, 8—10 mm. high, red-brown, gelatinous; spores of two kinds, thick-walled and thin-walled, broadly and obtusely bi-conical, scarcely constricted, smooth, brown, $40-50 \times 25-30\ \mu$; germ-pores four, two in each cell.

Æcidia on *Pyrus communis*, July—September; teleutospores on *Juniperus Sabina*, April and May. Not uncommon. (Fig. 234.)



Fig. 234. *G. Sabinae*. Groups of aecidia on leaf of Pear. $\times \frac{1}{2}$.

This is said to occur on other species of *Pyrus* and *Juniperus*. The life-history is similar to that of the other *Gymnosporangia*. The spermatogones are said by Fischer to have occurred on the fruit of the Pear; other authors record the aecidia on both the young fruits and the petioles. The aecidia are easily distinguishable from all the others, the upper part of the peridium, after dehiscence, looking very like the calyptra of *Polytrichum*; but the teleutospores are similar to those of *G. confusum*, the chief difference being that the thick-walled spores of the latter are rounded at the summit, not bluntly conical.

In this, as in all the similar cases, when the aecidium is found on its host, search should be made in the neighbourhood for the alternate host; the Juniper is often found in a neighbouring garden. Since it is always the teleutospore-mycelium that is perennial, the only successful remedy for this plant-disease is to destroy and burn the Juniper, or at least the affected part; it is useless to spray the aecidial host.

DISTRIBUTION: Europe.

CRONARTIACEÆ.

Nearly all heterœcious.

Teleutospores one-celled, without pedicels, produced in chains; the chains remaining united laterally into bundles which may be either columnar, wart-like or discoid; germinating when mature by typical basidia. All the sori subepidermal; spermogones are known in both genera.

Teleutospores in long chains, united into pulvinate sori; cell-wall smooth, colourless. Uredospores catenulate, surrounded by a very delicate evanescent peridium. Æcidia not known in the British species.

Chrysomyxa.

Teleutospores in long chains, united into columnar sori; wall smooth, slightly coloured. Uredospores borne singly on pedicels, echinulate, surrounded by a peridium which ruptures at the summit. Æcidia erumpent, inflated, with a membranous peridium which ruptures at the sides; æcidiospores partly smooth, not uniformly verrucose over the whole surface, owing to partial fusion of the warts.

Cronartium.

CHRY SOMYXA Unger.

Spermogones hemispherical. Æcidia with a well-developed peridium; æcidiospores with coarsely verrucose membrane, without germ-pores. Uredospores produced in rows by basipetal abstriction, resembling æcidiospores, but without or with a very delicate peridium. Teleutospores forming velvety pulvinate sori, in simple or branched chains, one-celled, with thin colourless membrane, germinating without a resting period.

In addition to the two species mentioned below, it is stated in Massee (Plant Diseases, p. 266) that the æcidium, named *Peridermium coruscans* (Fr.) and assigned by Tranzschel to a *Chrysomyxa* on *Ledum*, has been seen on *Picea Pinsapo* in England, doubtless on newly imported plants. It is common on

Picea excelsa in the North of Europe and has its uredo- and teleutospores on *Ledum palustre*, on which it produces witches'-brooms. See Klebahn, Wirts. Rost. p. 391. It is named by Tranzschel *Chrysomyxa Woronini*.

Quite recently also *Chrysomyxa Rhododendri* has been detected in Scotland by Mr D. A. Boyd. See Appendix.

1. *Chrysomyxa Empetri* Schröt.

Uredo Empetri Pers. ; Cooke, Handb. p. 527 ; Micr. Fung. p. 216.

Chrysomyxa Empetri Schröt. Krypt. Flor. Schles. iii. 372. Plowr.

Ured. p. 253. Sacc. Syll. vii. 762. Fischer, Ured. Schweiz, p. 557.

Melampsoropsis Empetri Arthur, N. Amer. Fl. vii. 118.

Uredospores. Sori hypophyllous, occasionally (according to Magnus) epiphyllous, small, roundish or elongated, sometimes arranged in lines parallel to the midrib, covered by the raised epidermis, orange; spores in short chains, ellipsoid or polygonal, densely verrucose, 26—35 $\times$ 18—25 μ , 30—35 $\times$ 21—28 μ (according to Fischer), 25—30 $\times$ 17—25 μ (Plowright), 26—37 $\times$ 18—26 μ (Arthur); wall rather thick, colourless; contents orange.

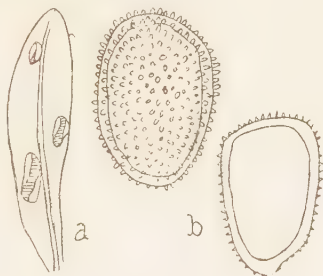


Fig. 235. *C. Empetri*. *a*, leaf of *Empetrum nigrum*, showing three uredo-sori, $\times 10$; *b*, uredospores $\times 600$.

On *Empetrum nigrum*. Uncommon; North Wales, etc. May—October. Often in small quantity, and very inconspicuous except when fresh. (Fig. 235.)

This fungus is considered to be a *Chrysomyxa* because the uredospores are produced in chains. The teleutospores seem doubtfully to have been observed by Rostrup and Lagerheim, and might possibly be discovered in this country if looked for. This parasite also occurs on the same host in the northern half of North America, but there also no teleutospores have ever been seen.

DISTRIBUTION: Europe, North America.

2. *Chrysomyxa Pyrolæ* Rostr.

Æcidium Pyrolæ DC. Flor. Fr. vi. 99.

Trichobasis Pyrolæ Berk.; Cooke, Handb. p. 529; Micr. Fung. p. 223 p.p.

Chrysomyxa Pyrolæ Rostr. Bot. Centr. iii. 126 (1881). Plowr. Ured. p. 253. Fischer, Ured. Schweiz, p. 429. Sacc. Syll. vii. 761.

Melampsoropsis Pyrolæ Arthur, N. Amer. Fl. vii. 118.

Uredospores. Sori hypophyllous, often covering the whole surface uniformly, roundish, $\frac{1}{2}$ —1 mm. diam., soon naked, surrounded by the torn epidermis and a very delicate evanescent peridium, yellow; spores in chains, roundish or polygonal, verrucose, orange, $21\text{--}28 \times 18\text{--}21 \mu$.

Teleutospores. Sori hypophyllous, covering the whole leaf-surface uniformly, up to $\frac{1}{2}$ mm. wide, roundish or oblong, flat, waxy, yellowish- then blood-red, when dry brown; spores ellipsoid, about 8μ wide, in rows as much as $100\text{--}120 \mu$ long.

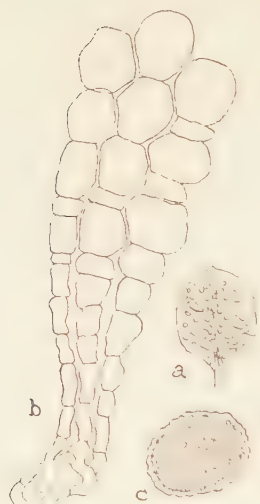


Fig. 236. *C. Pyrolæ*. a, uredosori, on underside of leaf, nat. size; b, chains of young uredospores, showing intercalary cells; c, mature uredospore. On *P. maritima* (Formby, ex herb. H. J. Wheldon).

On *Pyrola minor*, *P. rotundifolia* and its var. *P. maritima*. Uncommon: Edinburgh, Kew Gardens, Lancashire, etc. April—August. (Fig. 236.)

This parasite may possibly be heterœcious; Fraser (Mycologia, 1911, iii. 67) suggests that *Peridermium conorum-Piceæ* is its acidium; Rostrup, Arthur, and Kern had already expressed the same idea. The

teleutospores are rarely formed, and the fungus probably maintains itself by its uredospores, which can be distinguished from those of *Pucciniastrum Pyrolæ* by their sori being scattered (not in groups), and by the absence of a distinct peridium.

DISTRIBUTION: Europe, North America.

As the remarkable suggested acidium-stage may possibly be found in this country, it will be convenient to add here the description given of it, so as to aid in its identification :

PERIDERMIIUM CONORUM-PICEÆ

(*Æcidium conorum-Piceæ* Reess.)

Æcidia on the outer surface of the scales, large, $\frac{1}{2}$ cm. or more in diam., oblong or irregular in shape, one or two (or in any case few) on each scale, immersed, white ; spores ellipsoidal, orange, $28-35 \times 18-24 \mu$; epispore with numerous, large, crowded, prismatic warts, each about $3-4 \mu$ wide.



Fig. 237. *P. conorum-Piceæ*.
Æcidiospore, from scales of
Picea excelsa (after Fischer),
 $\times 600$.

On cones of *Picea excelsa*. August, September. In some years rather common in the Alps and Jura Mountains. (Fig. 237.)

CRONARTIUM Fries.

Spermogones hemispherical. Æcidia with a broad, inflated, irregularly torn peridium ; æcidiospores with a coarsely verrucose membrane, smooth on one side, without germ-pores, separated by well-marked intercalary cells. Uredo-sori enclosed in a hemispherical peridium which opens at the summit by a narrow pore ; uredospores produced singly, on pedicels, echinulate, without germ-pores. Teleutospores abstricted in long chains, and remaining united into cylindrical columns which are horny when dry, germinating as soon as mature. Basidiospores round, very minute.

1. *Cronartium asclepiadeum* Fr.

Cronartium asclepiadeum Fr. Obs. Myc. i. 220 (1815). Fischer, Ured. Schweiz, p. 431, f. 295. Sacc. Syll. vii. 597.

C. Paeoniae, Cast. Catal. Pl. Marseill. p. 217 (1845). Cooke, Micr. Fung. p. 215.

C. flaccidum Wint. Pilze, i. 236 (1884). Plowr. Ured. p. 254. Sacc. Syll. vii. 598.

Peridermium Cornui Kleb. Zeitschr. f. Pflanzenkr. 1892, ii. 269, pl. 5, f. 2.

Aecidiospores. Aecidia (*P. Cornui*) crumpeut from the bark, forming large reddish-yellow bladders, generally occupying a portion of a branch in large numbers; spores ellipsoid, $22-26 \times 16-20 \mu$; episporer $3-4 \mu$ thick, verrucose, thinner on part of its surface and there smooth or somewhat reticulate.

Uredospores. Sori small, pustular, surrounded by a peridium which opens at the summit with a pore; spores ellipsoid or ovate, sparsely echinulate, $21-24 \times 17-21 \mu$.



Fig. 238. *C. asclepiadeum*. a, *Peridermium Cornui* on branch of Pine; b, telento-sori on leaf of Peony (reduced); c, uredospore $\times 600$; d, part of a column of telentosporer $\times 300$.

Teleutospores. Sori cylindrical, often curved, arranged in large clusters, over 1 mm. high, brown, at length horny, compact; spores ellipsoid or cylindrical-oblong, reaching 56μ long and 14μ broad; episporer thin, slightly thicker above.

Aecidia on the branches of *Pinus silvestris*, May, June; uredo- and teleutospores on *Paeonia officinalis* in gardens, July–October. Very uncommon. (Fig. 238.)

It has been proved by the researches of Cornu, Klebahn, Fischer and many others, not only that the remarkable aecidia on Pine are genetically connected with the other spore-forms on Peony, but also that they can

produce the same on *Vincetoxicum*, *Nemesia*, *Cynanchum*, and *Verbena*, as well as on many species of *Paeonia*. There is reason for believing that the parasitism on *Nemesia*, at least, has arisen at a very recent date. This species is therefore plurivorous in its teleuto-stage, but not in its æcidial stage. The mycelium is perennial, according to Fischer, in the pine-branches; it produces æcidiospores in May and infects the alternate hosts, on which uredo- and teleutospores are borne during the summer—the latter can germinate at once.

2. *Cronartium Quercuum* Miyabe.

Uredo Quercus Brondeau in Duby, Bot. Gall. ii. 893 (1830). Cooke, Handb. p. 526; Micr. Fung. p. 216. Plowr. Ured. p. 257. Fischer, Ured. Schweiz, p. 539.

Peridermium deformans and *P. giganteum* Tubeuf, Pflanzenkr. p. 429.

Melampsora (?) *Quercus* Schröt.; see Sacc. Michel. ii. 308; Syll. vii. 594.

Cronartium asclepiadeum var. *Quercuum* Berk. Grevill. iii. 59 (from the U.S.). Sacc. Syll. vii. 597.

C. Quercuum Miyabe, Bot. Mag. Tokyo, xiii. 74 (1899).

C. Quercus Arthur, North Americ. Fl. vii. 122 (1907).

[*Æcidiospores*. *Æcidia* caulicolous, forming subglobose swellings 5—25 cm. across, arranged in tortuous lines or cerebroid, at first orange-yellow, bladdery; peridium colourless, circumscissile, soon falling away in flakes or sheets, about 2 cells thick, outer surface smooth, inner verrucose; cells roundish or irregularly compressed, walls very thick, lumen small; spores obovate, $25\text{--}32 \times 17\text{--}23 \mu$; wall colourless, uniformly thick ($2\frac{1}{2}\text{--}3\frac{1}{2} \mu$), coarsely verrucose, usually with smooth spot at base and extending up one side, tubercles somewhat deciduous.]



Fig. 239. *C. Quercuum*. Uredospores, on *Quercus* (ex herb. Thos. Brittain).

Uredospores. Sori hypophyllous, thickly scattered, round, small ($\frac{1}{4}$ mm.), hemispherical, dehiscing by an apical pore, at length surrounded by the torn epidermis, yellow; peridium delicate or wanting; spores obovate to broadly ellipsoid, orange-yellow, $15\text{--}25 \times 10\text{--}17 \mu$; wall colourless, 3μ thick, evenly echinulate with short strong points.

[*Teleutospores*. Sori hypophyllous, columnar, filiform, 2—3 mm. long, $150\text{--}175 \mu$ thick; spores fusiform to oblong, $30\text{--}40$

$\times 15-20 \mu$; wall nearly colourless, smooth, $2-3 \mu$ thick; basidiospores oval.]

[*Æcidia* on branches of *Pinus* ;] uredo- and teleutospores on leaves of *Quercus pedunculata*. Rare: Hastings, St Leonards, Shere, Hurstmonceaux, Salisbury. October. (Fig. 239.)

Only the uredospores have been found in this country, and usually so also on the continent. The *æcidia* have been found in the United States on five species of *Pinus*, as well as on others in Japan; and the other spore-forms on at least 20 species of *Quercus* in various localities. The description (except for the uredospores) is taken from Arthur (*l.c.*). The uredospores seem to be most common on the leaves of the shoots that spring up from the stools of felled oaks. They occur also in France and Switzerland in the same way. Their dimensions are smaller in this country than those given by Arthur.

DISTRIBUTION: Europe, United States, Guatemala, Japan.

3. *Cronartium ribicola* F. de Waldh.

Cronartium ribicola Fisch. de Waldh. in Rab. Fung. Eur. no. 1595; Hedwig. xi. 182. Klebahn, Wirtsw. Rostp. p. 382. Sacc. Syll. vii. 598. Fischer, Ured. Schweiz, p. 433, f. 296. Gard. Chron. ser. 3, xi. 736; xii. 44, 133, 137, 501; xiii. 425; xxiii. 202, 244; xxvi. 72-3, 94. Arthur, N. Amer. Fl. vii. 122.

Peridermium Strobi Kleb. Abhandl. Nat. Ver. Bremen, x. 153, pl. 1, f. 5-10, 13, 14; Zeitschr. f. Pflanzenkr. ii. 269, pl. 5, f. 1.

Spermogones. Irregular elevations of the bark, $2-3$ mm. broad, yellow, with a minute opening through which exudes a sweet fluid in which the spermatia are included; spermatia ovoid to elliptical, $2-4\frac{1}{2} \mu$.

Æcidiospores. *Æcidia* erumpent from the bark in the form of a bladder, with an inflated peridium, about 1 cm. high, yellowish-white; spores roundish or polygonal, coarsely verrucose, except on an elongated smooth patch, orange, $22-29 \times 18-20 \mu$; epispore $2-2\frac{1}{2} \mu$ thick, $3-3\frac{1}{2} \mu$ at the smooth spot.

Uredospores. Sori hypophyllous, small, pustular, forming orbicular groups $1-5$ mm. across, surrounded by a delicate peridium which opens at the summit with a pore; spores ellipsoid to obovoid, distantly and sharply echinulate, orange, $21-24 \times 14-18 \mu$; epispore colourless, $2-3 \mu$ thick.

Teleutospores. Columns hypophyllous, cylindrical, curved, up to 2 mm. long, crowded especially along the veins of the leaf, sometimes covering the whole leaf, orange to brownish-yellow; spores oblong, smooth, reaching $70\ \mu$ long $\times$ $21\ \mu$ broad.

Æcidia on stems and branches of *Pinus Cembra*, *P. monticola*, *P. Strobus*, March—June; uredo- and teleutospores on *Ribes nigrum*, *R. rubrum*, etc., July—October. Uncommon except when imported; Surrey, King's Lynn, Exeter, Westbury, Woburn, Windsor Forest, Perth, etc. (Fig. 240.)

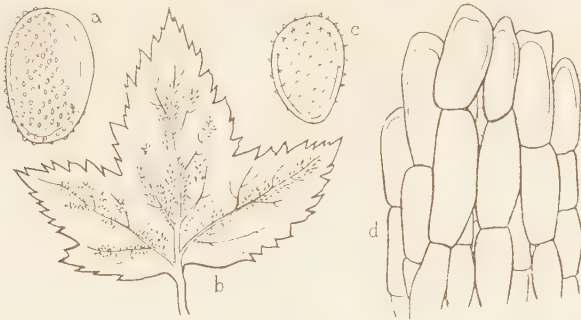


Fig. 240. *C. ribicola*. a, spore of *Peridermium Strobi*; b, the teleutospore-columns on leaf of Red Currant (reduced); c, uredospore; d, top of a column of teleutospores, $\times$ 600.

This dangerous parasite, sometimes called the Weymouth Pine Rust, is confined in its *æcidial* stage to the five-leaved Pines; it is reported on the continent also on *P. excelsa* and *P. Lambertiana*. The *æcidiospore* is distinguished from that of *Peridermium Pini* and *P. Cornui* by the fact that a great part of the surface is smooth. The attacked trees are stunted, the tops show a bushy growth that can easily be recognised; the part where the mycelium is growing is swollen. In the Currant, the attacked leaves become thicker in texture, and different in colour.

It was first discovered, in this country, at King's Lynn by Dr Plowright, who found the *Cronartium* on leaves of black, white, and red currant on July 3, 1892. On August 13 he exhibited in London a branch of *P. Strobus* affected by the mycelium of the alternate stage; the tree grew about fifteen yards away from the currant bushes. On March 19, 1893, he found the *Peridermium* in full perfection at the same place.

Though the *æcidium* occurs in Europe chiefly on the Weymouth Pine (*P. Strobus*), yet that cannot be its original host, since neither *Cronartium ribicola* nor *Peridermium Strobi* was found in America (the home of *P. Strobus*) until the fungus was imported on it from Germany. *P. Cembra*,

the Swiss Stone Pine, however, will equally serve as host, as has been shown by Tranzschel, and it has been found on that tree in Russia and in Switzerland. One of these countries was probably the original home of the parasite, from which it is spreading wherever its hosts will grow.

This is one of the species with which attempts have been made to produce infection by the use of the abundant spermatia (Klebahn, Wirtsw. Rost. p. 387), but numerous trials on healthy Weymouth Pines were entirely without result.

DISTRIBUTION: Europe (north of the Alps), Siberia, Japan, North America.

COLEOSPORIACEÆ.

Æcidium furnished with a peridium. Spermatogones sub-epidermal, flattish, linear, without ostiolar filaments, dehiscing by a slit. Teleutospores in one (more rarely two) subepidermal layers, dividing as they mature into four superimposed cells, each of which germinates by a sterigma bearing one basidiospore.

COLEOSPORIEÆ. Heterœcious.

Æcidia (*Peridermium*) more or less cylindrical, with inflated peridium, irregularly torn at summit. Uredospores abstricted in chains. Teleutospores with a strongly thickened gelatinous wall above. Basidiospores ovate. *Coleosporium*.

OCHROPSOREÆ. Heterœcious.

Æcidia with cup-shaped peridium. Uredospores abstricted singly. Teleutospores thin-walled. Basidiospores fusiform. *Ochropsora*.

ZAGHOVANIÆ. ABHÆCIOUS.

For the present, the abnormal genus *Zaghouania* may be arranged as a subfamily of the Coleosporiaceæ; it is distinguished especially by the fact that the four-celled basidium is formed internally, but emerges from the teleutospore before the formation of the round basidiospores. See p. 331.

Zaghouania.

The internal "basidium" which has been considered as a character of this family is not confined to it, being found also in *Chrysopsora*, which belongs to the Pucciniaceæ. It is remarkable that no species of the family has up till now been discovered in Australia, while only one of the Eurasian species

is indigenous to North America. This family retains probably, in the mode of germination of its teleutospore, a very primitive character, but has nevertheless undergone a large amount of recent evolution, and is no doubt worthy of subdivision.

There is a North American species, belonging to the Coleosporiaceæ, which is deserving of great attention. It is *Gallowaya Pini* Arthur (formerly *Coleosporium Pini* Galloway), which has teleutospores only, and on leaves of *Pinus inops*, i.e. on trees of the same order on which *Coleosporium* has its æcidia. Similarly, among the Melampsoraceæ, there is a like case in *Necium Farlowii* Arthur, which has its teleutospores on *Abies canadensis*, while various heterœcious Melampsoraceæ, with similar teleutospores on other (non-coniferous) plants, have their æcidia on Conifers. Again in the Cronartiaceæ, *Chrysomyxa Ledi* and *C. Rhododendri* are heterœcious species having their æcidia on *Picea excelsa*; but there is also *C. Abietis* having its teleutospores on the same host (*P. excelsa*) and no other spore form. *Gymnosporangium bermudianum*, already mentioned (p. 304), furnishes a somewhat similar instance. The evolutionary significance of these facts has not yet been elucidated.

COLEOSPORIUM Lév.

Æcidia with a more or less cylindrical inflated peridium, which opens by a cleft and becomes irregularly torn; æcidiospores with colourless membrane, without germ-pores, superficially tuberculate, the tubercles somewhat deciduous. Uredospores not enclosed in a peridium, abstricted in short chains, resembling the æcidiospores. Teleutospores in flat, waxy, indehiscent sori, with a colourless gelatinous membrane, which is thin and wavy at the sides but strongly thickened above, at first filled with a rich orange-red oily mass; at length each spore divides into four superimposed cells, which in autumn can germinate *in situ* as soon as mature, with a long sterigma.

The species of *Coleosporium* are morphologically very much alike, and are distinguished chiefly by their hosts. Moreover,

since the æcidia of all of them live on needles of two-leaved Pines, it is impossible to say where any given æcidium of this class belongs, without culture-experiments. If a *Coleosporium* can be found in the immediate neighbourhood, the æcidium may be conjecturally assigned to that. But though the æcidia are very much alike, there are certain differences to be seen, although nothing is yet known about their constancy as specific characters. In certain cases nearly all the peridia will be found on *one only* of the two leaves of Pine in each fascicle; this is, according to my experience, almost always true of *C. Senecionis*. In others, the peridia occur on *both leaves* of the fascicle; this seems to be the case usually with *C. Tussilaginis*. Some peridia are very bladdery and inflated, others are more flat or cylindrical. It may be possible in the future to distinguish them by these means, especially since the *Coleosporia* lend themselves easily to artificial cultures; see under *C. Rhinanthacearum* and *C. Tussilaginis*.

1. *Coleosporium Senecionis* Fr.

Uredo farinosa var. *Senecionis* Pers. Syn. p. 218.

Peridermium Pini Chev.; Cooke, Handb. p. 535 p.p., f. 219; Mier. Fung. pl. 2, f. 27, 28 (not the description p. 194).

P. acicolum Link.; Cooke, Mier. Fung. p. 194.

Puccinia glomerata (uredospores) Cooke, Handb. p. 500.

Coleosporium Senecionis Fr. Summ. Veg. Scand. p. 512. Cooke, Mier. Fung. p. 218, pl. 7, f. 145, 146. Plowr. Ured. p. 248 p.p. Sacc. Syll. vii. 751. Fischer, Ured. Schweiz, p. 451. Arthur, N. Amer. Fl. vii. 94.

Spermogones. Amphigenous, scattered, conspicuous.

Æcidiospores. Æcidia (*Peridermium acicolum*) oblong or shortly cylindrical, fragile, rupturing irregularly, whitish; spores almost all oblong, seldom roundish, densely verrucose, orange, $25-35 \times 15-25 \mu$.

Uredospores. Sori hypophyllous, roundish or on the stems elongated, soon naked and pulverulent, orange; spores mostly oblong, verruculose, $26-31 \times 14-17 \mu$; epispore rather thick.

Teleutospores. Sori hypophyllous, forming little red crusts; spores prismatic, length up to 100μ , breadth $18-24 \mu$; epispore at summit up to 22μ thick.

Æcidia on (?one of the two) leaves of *Pinus austriaca*, *P. silvestris*, May, June; uredo- and teleutospores on *Senecio Jacobaea*, *S. palustris*, *S. silvaticus*, *S. viscosus*, *S. vulgaris*, all through the year; also recorded for *S. pulcher*, *S. sarracenicus*, etc., in Botanic gardens, and on cultivated Cinerarias (i.e. *Senecio*) at Sydenham; see Journ. Roy. Hort. Soc. 1908, xxxiii. 511. Very common. (Figs. 241, 242.)



Fig. 241. *C. Senecionis*. a, chain of uredospores; b, two fascicles of leaves of *P. silvestris*, bearing peridia on one leaf only of each fascicle (reduced).



Fig. 242. *C. Senecionis*. Teleutospore germinating.

This is the species of *Coleosporium* whose life-history has been longest known; Wolff first experimentally demonstrated it in 1872, and he was followed by Plowright in 1882, as well as by Cornu, Hartig, Rathay, Von Thümen, Rostrup, Klebahn and Fischer. The *æcidium* had previously been called *Peridermium*. Since *Senecio vulgaris* continues to live through the winter in our climate, and Magnus and others have found the uredospores throughout the year, the intervention of the alternate host is not in this case necessary. Yet it is generally quite easy to find the *Peridermium* on the needles of *P. silvestris* if one searches in June any trees that may be growing in the neighbourhood of Groundsel infected with the parasite; since the *Peridermium* is not conspicuous, it may easily be overlooked unless special search is made. It is probable that there are several biological races of this fungus, on different species of *Senecio*, and it has been proved by Fischer that it cannot be transferred to *Cacalia* or *Sonchus*.

Since there are other so-called "species" of *Peridermium* on the leaves of *P. silvestris*, which are morphologically not distinguishable from that belonging to this species, it is always advisable, when such a one is found, to look on the possible hosts in the neighbourhood for the corresponding *Coleosporium*. But the *Peridermium* found on the bark of Scots Pine is totally distinct, both morphologically and biologically, although Wolff and Plowright recorded them as identical. Plowright, however, failed to infect *S. vulgaris* by spores from "a specimen of *Æc. Pini* on the bark of a young fir-branch" (i.e. pine-branch)—naturally enough; and he also puts on record (*l.c.* p. 250) his frequent failures to infect the Groundsel with spores from æcidia (*Æc. Pini* var. *acicola*) which seemed to him to be like those with which he succeeded. His consequent suspicion, that "there must be more than one species included under this name," is now abundantly confirmed. He was experimenting, in these latter cases, with æcidia belonging to some of the species of *Coleosporium* mentioned in the following pages.

In North America, *C. Senecionis* has been found on *S. vulgaris*, apparently in one locality only (Rhode Island), probably introduced from Europe; the *Peridermium* was not observed. In that quarter of the globe there are many indigenous species, biologically resembling ours, but mostly on different hosts, including one on a species of Orchidaceæ.

This fungus does not do much harm to the Pine, but in any case the removal of *Senecio* from the neighbourhood arrests the disease. The teleutospores germinate in the autumn in which they are produced.

DISTRIBUTION: Europe, North America (once).

2. *Coleosporium Tussilaginis* Tul.

Uredo Tussilaginis Schum. Pl. Säll. ii. 229.

Coleosporium Tussilaginis "Lév." in Tul. Mém. Ured. 1854, p. 136.

Cooke, Handb. p. 520, f. 211; Micr. Fung. p. 217, pl. 8, f. 180—2.

Fischer, Ured. Schweiz, p. 449.

C. Sonchi Plowr. Ured. p. 250 p.p. Sacc. Syll. vii. 752 p.p.

Peridermium Plowrightii Kleb. Zeitschr. f. Pflanzenkr. ii. 258, pl. 5, f. 6.

Æcidiospores. *Æcidia* (*P. Plowrightii*) like those of the allied species; spores oval or mostly round, delicately verrucose, $20-30 \times 15-24 \mu$.

Uredospores. Sori hypophyllous, small, scattered or aggregate, orange; spores roundish, very densely verruculose, $23-28 \times 17-21 \mu$; epispore rather thick.

Teleutospores. Sori filling large intercellular spaces of the mesophyll towards the lower surface of the leaf; spores prismatic, length up to 140μ , breadth $18-28\mu$; epispore $18-21\mu$ thick, or more, at the summit.

Æcidia on (?both) leaves of *Pinus silvestris*; uredo- and teleutospores on *Tussilago Farfara*, May—November, very common. (Fig. 243.)

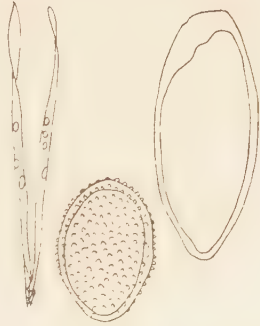


Fig. 243. *C. Tussilaginis*. *Æcidia* on both leaves of a fascicle of *P. silvestris* (from Blackman's experiment), reduced; uredo- and young teleutospore $\times 600$.

The connection of the spore-forms on the alternate hosts has been demonstrated by Plowright, Klebahn, Fischer and Wagner. Klebahn and Fischer showed moreover that the parasite cannot be transferred to *Petasites* or *Sonchus*.

Plowright produced the *æcidia* (*P. Plowrightii*) on leaves of Scots Pine from the *Coleosporium* on *Tussilago* (experiment 1243), 25th May, 1899. His specimens show the peridia, in almost every case, on both leaves of the fascicle. The same is true of the following experiment by Blackman: In October, 1904, he tied leaves of Coltsfoot bearing germinating teleutospores of *C. Tussilaginis* on four trees of *P. silvestris* at Crockham Hall, Kent. On April 14th, 1905, the beginnings of spermatogones and *æcidia* were visible in three cases on neighbouring needles, but nowhere else. In June, 1905, all four showed the *Peridermium*. Specimens in Herb. Kew.

The uredospores are often very densely and rather coarsely verruculose, but also occasionally smooth either wholly or in parts; in fact the warts are deciduous and may disappear entirely.

DISTRIBUTION: Europe.

3. *Coleosporium Petasitis* Lév.

Coleosporium Petasitis Lév. Ann. Sci. Nat. 1847, p. 373. Cooke, Handb. p. 521; Micr. Fung. p. 217. Fischer, Ured. Schweiz, p. 450.

C. Sonchi Plowr. Ured. p. 250 p.p. Sacc. Syll. vii. 752 p.p.

Peridermium Boudieri Fischer, Contrib. étude du genre *Coleosporium*, in Bull. Soc. Bot. Fr. xli. 171.

Æcidiospores. *Æcidia* (*P. Boudieri*) like those of neighbouring species.

Uredospores. Sori scattered, orange, at first covered by the epidermis, soon pulverulent; spores ovate or ellipsoid, densely and evenly verruculose, $21-34 \times 14-21 \mu$.

Teleutospores. Sori forming little red crusts; spores prismatic, length up to 100μ , breadth $18-24 \mu$; epispore up to 14μ thick at the summit.

Aecidia on leaves of *Pinus silvestris*; uredo- and teleutospores on *Petasites officinalis*, August—November, not uncommon.

The life-cycle has been demonstrated by Fischer and Wagner for *P. officinalis*: the parasite may also extend to other species of *Petasites*.

DISTRIBUTION: Europe.

4. *Coleosporium Sonchi* Lév.

Uredo Sonchi Pers. Syn. Fung., p. 217.

Coleosporium Sonchi Lév. Ann. Sci. Nat. 1847, p. 373. Cooke, Handb. p. 521; Micr. Fung. p. 218, pl. 8, f. 178, 179. Plowr. Ured. p. 250 p.p. Sacc. Syll. vii. 752. Fischer, Ured. Schweiz, p. 453.

Peridermium Fischeri Kleb. Zeitschr. f. Pflanzenkr. v. 13.

Spermogones } *Aecidia* (*P. Fischeri*) and spermogones like
Aecidiospores } those of neighbouring species: spores ellipsoid or polygonal-roundish, verrucose, $25-32 \times 18-25 \mu$.



Fig. 244. *C. Sonchi*. On *S. arvensis*. Two chains of young uredospores; teleutospore, showing fusion-nucleus; and uredospore.

Uredospores. Sori small, round or oblong, girt by the epidermis, in irregular groups, especially along the veins, yellowish-orange; spores roundish-oval, densely and finely verruculose, $18-25 \times 15-21 \mu$.

Teleutospores. Sori forming small, flat, roundish, waxy-red crusts; spores prismatic, length reaching 100μ , breadth $18-30 \mu$; epispore at summit reaching 18μ thick.

Æcidia on leaves of *Pinus silvestris*; uredo- and teleutospores on *Sonchus arvensis*, *S. asper*, *S. oleraceus*, August—November, not uncommon. (Fig. 244.)

Klebahn, Fischer, and Wagner have demonstrated the life-cycle of this parasite; the two former have also proved that it cannot be transferred to *Cacalia*, *Campanula*, *Senecio*, or *Tussilago*. Fischer records this species on *Sonchus palustris* as well as on the hosts given above.

DISTRIBUTION: Europe.

5. *Coleosporium Cacaliæ* Fekl.

Uredo Cacaliæ DC. Flor. fr. vi. 65.

Coleosporium Cacaliæ Fekl. Symb. Myc. p. 43. Cooke, Micr. Fung. p. 218. Fischer, Ured. Schweiz, p. 446.

C. Sonchi Plowr. Ured. p. 250 p.p.

Peridermium Magnusianum Fisch. Contrib. étude du genre *Coleosporium*, in Bull. Soc. Bot. Fr. xli. 171.

P. Magnusii Wagner, Zeitschr. f. Pflanzenkr. vi. 9 and viii. 257.

[*Spermogones* | Resembling those of other *Coleosporia*.]
[*Æcidiospores* |

Uredospores. Sori numerous, roundish, at first covered by the epidermis, at length pulverulent, orange; spores ellipsoid, verruculose, deep-yellow, $24-35 \times 21-24 \mu$.

Teleutospores. Sori hypophyllous, forming flat, red, waxy crusts; spores prismatic, up to 140μ long, $18-25 \mu$ broad, thickened (up to 28μ) at the summit.

[*Æcidia* on leaves of *Pinus montana*, perhaps also of *P. silvestris*;] uredo- and teleutospores on *Cacalia hastata*, *C. suaveolens*. The spermogones and *æcidia* have not been observed in Britain; the other spore-forms at Bath (Rev. J. E. Vize),

Bathaston (C. E. Broomer), Oxford Botanic Gardens (Herb. Buxant), October. This is, of course, an introduced species.

DISTRIBUTION: Europe.

6. **Coleosporium Rhinanthacearum** Lév.

Coleosporium Rhinanthacearum Lév. Ann. Sci. Nat. 1847, p. 373.

Cooke, Handb. p. 521; Micr. Fung. p. 218, pl. 8, f. 176, 177.

C. Euphrasiae Plowr. Ured. p. 252. Sacc. Syll. vii. 754.

This species is now divided into two, but on purely biological grounds: no morphological distinctions worthy of the name can be discerned, and since the hosts are all closely allied it is perhaps best to retain the collective name—at any rate for a time.

(1) **COLEOSPORIUM EUPHRASIAE** Wint.

Uredo Euphrasiae Schum. Pl. Säll. ii. 230.

Coleosporium Euphrasiae Winter. Pilze, p. 246. Fischer, Ured. Schweiz, p. 442.

Peridermium Stahlianii, Kleb. Zeitschr. f. Pflanzenkr. ii. 269, pl. 5, f. 5.

Sporangiospores—Like those of the allied species. *Aecidia*—

spores oval or roundish, $20-30 \times 15-24 \mu$.

Uredospores. Sori small, scattered, roundish, flat, yellowish-red; spores irregularly polygonal, densely verruculose, $20-24 \times 14-17 \mu$; epispore thin, colourless.

Teleutospores. Sori small, flat, roundish, red; spores prismatic, orange, up to 105μ long, $18-24 \mu$ wide; epispore at summit about 14μ thick.

Aecidia on leaves of *Pinus silvestris*; uredo- and teleutospores on *Euphrasia officinalis*, *Bartsia Odontites*, *Rhinanthus Cristagalli*, July—September, very common.

It is not certain that *Bartsia* can be infected from *Euphrasia* or *Rhinanthus*; no experiments on that point are recorded. Klebahn proved abundantly that the parasite can be transferred from *Rhinanthus* to *Euphrasia*, but not to *Senecio*, *Sonchus*, or *Tussilago*. Wagner (Zeitschr. f. Pflanzenkr. viii. 261) infected *Euphrasia* with aecidiospores from *Pinus*

(2) *COLEOSPORIUM MELAMPYRI* Karst.

Uredo Melampyri Rebentisch, Flor. Neomarch. p. 355.

Col. Melampyri Karst. Myc. Fenn. iv. 62. Fischer. Ured.

Schweiz, p. 440, f. 269.

Peridermium Soraueri Kleb. Zeitschr. f. Pflanzenkr. iv. 194.

The only apparent differences from *C. Euphrasiae* are in the size of the spores: uredospores $24-35 \times 21-28 \mu$; teleutospores as much as 115μ long, $21-28 \mu$ wide; episporium very thick (up to 28μ) at the summit.

Aecidia on leaves of *Pinus silvestris*; uredo- and teleutospores on *Melampyrum arvense*, *M. pratense* and its var. *montanum*, July—September, not uncommon. (Fig. 245.)

Wagner records the *aecidium* also on *P. montana*. Klebahn has demonstrated that the spores of this species will not infect *Euphrasia*, *Rhinanthus*, or *Campanula*. I have not seen the thickening on the summit of the teleutospores so pronounced in ours as in the continental specimens, possibly because they were not so mature.

Since the uredo-hosts of *C. Rhinanthacearum* are all annual and die at the approach of winter, it would seem probable that fresh infections must occur each year from the *aecidium*, but as this is, at any rate, not commonly found, the *aecidiospores* must be widely distributed by the wind; it is very possible, however, that the fungus winters in some other manner as yet unsuspected, or that the *aecidia* are more abundant than is thought to be the case. They should be searched for in May and June. There is here great scope for experimental research, especially since young pot-plants of *Pinus* can be used for infection. Klebahn placed such a Pine amongst a clump of *Melampyrum*, strongly infested with *Col. Melampyri*, and left it from July to September the pot sunk in the earth; in the latter month spermatogones appeared and the *aecidium* *Peridermium Soraueri*, in the following spring.

DISTRIBUTION: Europe.

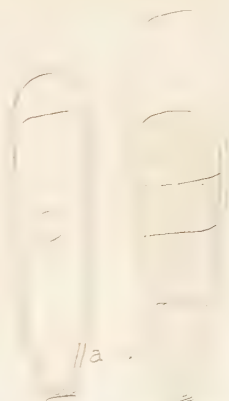


Fig. 245. *C. Melampyri*.
a, teleutospore on *M. pratense*, Randan Woods;
b, teleutospore on the same, gathered at Bonn, Germany.

7. *Coleosporium Campanulae* Lév.

Uredo Campanulae Pers. Syn. p. 217.

Coleosporium Campanulae, Lév. Ann. Sci. Nat. ser. 3, viii. 373.

Cooke, Handb. p. 521; Micr. Fung. p. 218. Plowr. Ured. p. 251.

Sacc. Syll. vii. 753. Fischer, Ured. Schweiz, p. 443. Arthur, N. Amer. Flor. vii. 88.

Peridermium oblongisporium Fekl. Symb. Myc. p. 42. Rostr. Bot.

Tidsskrift, xix. pp. 40, 41, 49.

P. Rostrupii Fischer in Bull. Soc. Bot. Fr. xli. p. clxxii.

Spermogones. Amphigenous, scattered, conspicuous.

Æcidiospores. *Æcidia* (*Peridermium oblongisporium*) like those of allied species, but spores distinctly oblong, $34-40 \times 18-22 \mu$ (?).



Fig. 246. *C. Campanulae*. a, uredosori on *C. rotundifolia*, nat. size; b, uredospore and young and mature teleutospores, on *C. glomerata*, $\times 600$.



Fig. 247. *C. Campanulae*. Teleutospores, beneath the epidermis, $\times 360$; and uredospore $\times 600$. On *C. rotundifolia*.

Uredospores. Sori hypophyllous, scattered, often confluent, covering the whole leaf-surface, also on the stems, roundish or irregular, covered by the epidermis for some time, then naked, yellow or yellowish-red, fading to whitish; spores ellipsoid to oblong, subangular, strongly and rather densely verruculose, orange, $21-35 \times 14-21 \mu$.

Teleutospores. Sori hypophyllous, subepidermal, scattered, often confluent, forming small, flat, red, then pale-brownish crusts; spores prismatic, up to 100μ long, $21-28 \mu$ wide; epispore hyaline, reaching 35μ at the summit, but thin elsewhere.

Æcidia on leaves of *Pinus silvestris*; uredo- and teleutospores on *Campanula glomerata*, *C. latifolia*, *C. rotundifolia*, *C. Trachelium*, *C. turbinata*, end of July—October, not uncommon; sometimes abundant on cultivated species of *Campanula*, in both uredo- and teleuto-stages. (Figs. 246, 247.)

Some of the forms on the various species are separated by Klebahn as biologically distinct, but the specialisation is not in any case sharply fixed (Wirtwechs. Rostp. pp. 365—9). *C. Campanulæ* is also recorded, in other countries, on many other species of *Campanula* and on *Phyteuma* and *Specularia*. In North America the *æcidia* are found on *Pinus rigida* but, as in this country, are much less common, or at least less frequently observed, than the spore-forms on *Campanulaceæ*. On *C. rotundifolia*, this species and *Puccinia Campanulæ* may be found in company.

DISTRIBUTION: Europe, North America, China, Japan, East Indies.

OCHROPSORA Dietel.

Æcidia with cup-shaped peridium. Uredospores solitary, on pedicels. Teleutospores united loosely into waxy crusts, club-shaped or cylindrical, not thickened above, dividing as they mature into four superimposed cells.

This genus is not closely allied to *Coleosporium*. It is, indeed, doubtful whether the character upon which the *Coleosporiaceæ* are united into one group, viz. the internal basidium, is really an indication of close affinity. There can be little doubt that *Chrysopsora*, which also has an internal basidium, belongs to the *Pucciniaceæ*, and not to the *Coleosporiaceæ*.

Ochropsora Sorbi Diet.

Æcidium leucospermum DC. Flor. fr. ii. 239. Cooke, Handb. p. 536;

Micr. Fung. p. 194, pl. 1, f. 4 -6. Plowr. Ured. p. 269.

Ochropsora Sorbi Dietel, Ber. Deutsch. Bot. Gesell. 1895, xiii. 401.

Fischer, Ured. Schweiz, p. 455.

Spermogones. On the foliage leaves (loosely spread over the whole upper surface) and even on the sepals, whitish, then brownish.

Æcidiospores. Æcidia scattered pretty regularly over the lower surface of the leaves, not very crowded, shortly cylindrical, white, with torn revolute margin; spores irregularly oblong, colourless, thin-walled, very delicately verruculose, $18-30 \times 15-21 \mu$.

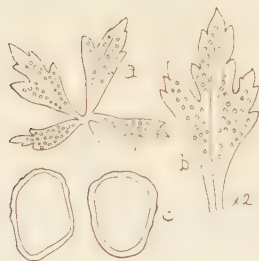


Fig. 248. *O. Sorbi*. *Æcidium leucospermum*. *a*, æcidia on leaf of *A. nemorosa*, nat. size; *b*, the same, $\times 2$; *c*, æcidiospores, $\times 600$.

[*Uredospores.* Sori hypophyllous, small, roundish, scattered, not more than $\frac{1}{4}$ mm. diam.; spore-mass greyish or yellowish-white, surrounded by a circle of paraphyses, which form a kind of peridium, but their upper ends, when mature, are free and sub-

clavate; spores subglobose to ovate, pale-brownish, distantly verrucose, $25-28 \times 18-25 \mu$; episore $1-1\frac{1}{2} \mu$ thick, with no perceptible germ-pores.

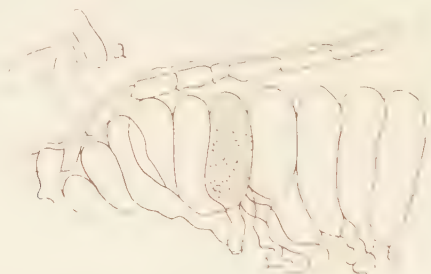


Fig. 249. *O. Sorbi*. Section of teleuto-sorus, before the division of the spores into four cells (one spore is shaded); *a*, basidiospores. (After Fischer.)

Teleutospores. Sori hypophyllous, $\frac{1}{4}-\frac{1}{2}$ mm. diam., at first covered by the epidermis, pustulate, pale flesh-colour, roundish or oblong, clustered in groups; spores cylindrical, rounded above, crowded, grey, granular, subopaque, $70 \times 10-18 \mu$, at length divided into four cells; basidiospores fusiform, $22-25 \times 8 \mu$.]

Æcidia on *Anemone nemorosa*, April—June, not common, Oxford, Cambridge, Devon, North Wales, Yorkshire, Scotland, etc. [Uredo- and teleutospores on *Pyrus Aucuparia*, August and September, not yet observed in Britain.] (Figs. 248, 249.)

The description of the uredo- and teleutospores is after Fischer; the latter mature in autumn and germinate at once. According to him, the mycelium of the æcidial stage is perennial in the rhizome, but Klebahn proved (Zeitschr. f. Pflanzenkr. 1907, p. 144) that the teleutospores infect the growing points of the rhizome in autumn, and produce the æcidia in the following spring. He could also infect other species of *Pyrus* (*Aria*, *torminalis*, *scandica*, *Malus*) from the Anemone; Fischer did the same for *P. fennica* and *P. communis*. In the Anemone nearly every leaf of the affected plant will be attacked, as well as the flower-shoots. The leaves become longer, narrower and of a paler green, and are borne on longer petioles. They are often divided into more segments than the normal leaves. Fischer remarks that, when the fungus appears on the sepals, the cells in the neighbourhood develop chloroplasts.

The discovery of this heterœcism was due to Dietel and was confirmed by Klebahn; previously the æcidium has been mistakenly attributed, by Soppitt, to *Endophyllum* as *E. leucospermum*. The mode of germination of the spores will, of course, easily distinguish them: about this there seems to have been some misapprehension—Soppitt (Journ. Bot. 1893, p. 274) distinctly stated that the spores did not germinate with “promycelial” spores, but in the Trans. Brit. Myc. Soc. i. 84, 98, this is altered into the statement that the spores “germinate as do those of the (other) *Endophylla*.”

Puccinia fusca lives upon the same plant (*Anemone nemorosa*) but affects its host in a different way (see p. 215). *Æcidium punctatum*, a stage of *Puccinia Pruni-spinosae*, is found on *A. nemorosa* as well as on garden Anemones (*A. coronaria*), but differs in the character of the broader peridium and in having faintly coloured spores. Moreover, its spermogones are dark-coloured and are found on both sides of the leaf (see p. 207).

ZAGHOUANIA Patouillard.

Sori erumpent, subpulverulent. *Æcidia* (*Peridermium*) with a peridium which is irregularly lacerate above; margin slightly involute; spores in short chains, soon seceding. Spermogones flask-shaped, with ostiolar filaments. Uredospores pedicellate, solitary. Teleutospores one-celled, ovoid, pedicellate, with a slightly thickened hyaline and verruculose epispore, germinating as soon as mature; basidium four-celled, semi-internal; basidiospores nearly sessile.

The description is founded upon that given by Dumée and Maire in Bull. Soc. Myc. Fr., 1902. The semi-internal basidium is characteristic. Dumée and Maire make a separate family,

Zaghouaniaceæ, for its reception and compare it to *Septobasidium* among the Auriculariæ; it seems more likely that *Zaghouania* will be proved to belong to the Pucciniaceæ.

Zaghouania Phillyreæ Pat.

Æcidium Phillyreæ DC. Flor. fr. vi. 96. Sacc. Syll. vii. 807. Massee, Journ. Bot. 1908, xlv. 153. Trans. Brit. Myc. Soc. iii. 123.

Æ. crassum var. *Phillyreæ* Cooke, Handb. p. 539.

Uredo Phillyreæ Cooke, Exsicc. i. 592. Plowright, Ured. p. 258. Sacc. Syll. vii. 856.

Zaghouania Phillyreæ Pat. Bull. Soc. Myc. Fr. 1901, xvii. 187. Dumée et Maire, Bull. Soc. Myc. Fr. 1902, xviii. 23.

Spermogones. Flask-shaped, with well-developed ostiolar filaments; spermatia ovoid, hyaline, $4-5 \times 2-3 \mu$.

Æcidiospores. *Æcidia* numerous, densely crowded, semi-immersed, with a more or less involute, nearly entire, whitish margin; spores variable, globose, ovoid or oblong-pyriform, alveolate-reticulate, deep orange-yellow, $20-30 \times 14-18 \mu$.

Uredospores. Sori hypophyllous, usually on yellowish spots, solitary or aggregated, subangular, at length naked, orange-yellow; spores globose

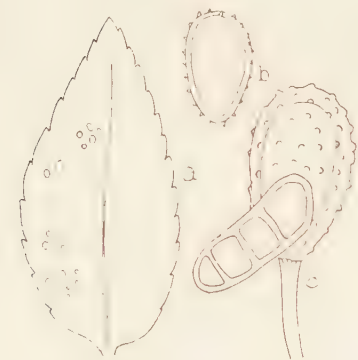


Fig. 250. *Z. Phillyreæ*. a, uredo-sori on leaf of *P. media*, Chichester, nat. size; b, uredospore from the same; c, teliospore beginning to germinate (after Dumée and Maire).

to ovoid, echinulate, orange-yellow, $24-32 \times 12-16 \mu$.

[*Teleutospores*. Mixed with the uredospores, oblong-ovoid, $45-65 \times 15-18 \mu$, with a rather thick, hyaline, verruculose epispore; basidiospores sessile, smooth, subglobose, $12-14 \mu$ diam.]

Æcidia on leaves and young shoots of *Phillyrea latifolia*, Pevensey Churchyard, August, 1907 (G. Massee); on *Phillyrea media*, near Chichester, *acidia*, 1869, *uredo*, April, 1874 (F. Paxton). The uredospores have been gathered in Italy as early as February. (Fig. 250.)

The fungus in the æcidium-stage forms rounded swollen pustules on the leaves or extensive patches on the stems. Every shoot of the year is usually attacked and contorted, and in August is covered and made conspicuous by a copious development of the orange spores. The teleutospores have not been detected in this country. They are remarkable for their mode of germination—the basidium is formed internally as in *Colcosporium*; this then emerges through a rupture at the base of the spore and produces its large nearly sessile basidiospores externally, one from each cell.

DISTRIBUTION: France, Germany, Italy, Corsica, Tunisia, Algeria.

ENDOPHYLLACEÆ

Teleutospores in long chains, surrounded by a peridium, which is formed like that of a typical æcidium of *Puccinia* from the peripheral cell-rows, but is sometimes less strongly developed; spores separated by intercalary cells, produced from a fusion-cell, but germinating as soon as mature by a typical basidium and basidiospores; germ-pores not perceptible; spore-wall coloured, verruculose. Spermatogones present; both kinds of sori subepidermal.

ENDOPHYLLUM Lévêillé.

Characters of the genus the same as of the family.

1. **Endophyllum Euphorbiæ-silvaticæ** Wint.

Æcidium Euphorbiæ-silvaticæ DC. Flor. fr. ii. 241.

Æ. Euphorbiæ Pers.; Cooke, Handb. p. 537; Micr. Fung. p. 195 p.p.

Endophyllum Euphorbiæ-silvaticæ Winter, Pilze, i. 251. Sacc. Syll. vii. 767. Fischer, Ured. Schweiz, p. 437, f. 298.

E. Euphorbiæ Plowr. Ured. p. 228.

Spermatogones. Epiphyllous, or a few amongst the æcidia, yellowish, then brown.

Teleutospores. Sori hypophyllous or occasionally epiphyllous, more or less covering the whole surface, crowded, æcidium-like, sunk in the leaf-tissue which is slightly swollen, surrounded by a thin peridium in the shape of a shallow cup, with a short,

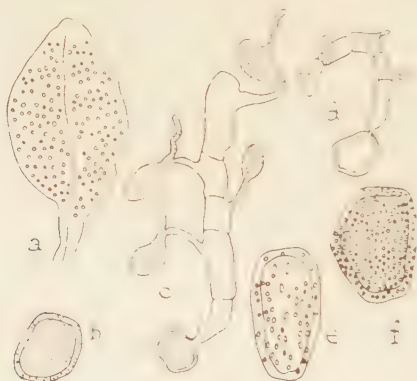


Fig. 251. *E. Euphorbiae-silvaticae*. *a*, affected leaf of *E. amygdaloides*, nat. size; *b*, æcidio-teleutospore; *c*, germinating spore; *d*, another, not so advanced, $\times 540$; *e*, inner, and *f*, outer wall of peridium-cell, $\times 600$.

torn, slightly revolute margin; spores in evident chains, bluntly polygonal or subglobose, densely but finely verruculose, orange, $18-23\mu$; episporium about 1μ thick; basidiospores obovate, yellow.

On *Euphorbia amygdaloides* (= *E. silvatica*). Rather uncommon. April—June. (Fig. 251.)

The mycelium usually perennates in the plant. The affected shoots are taller than the normal ones, with shorter, wider and paler leaves; they seldom flower. This species externally closely resembles an æcidium, and can be distinguished from one only by the different mode of germination of the spores. The æcia which occur on other species of *Euphorbia* belong to different life-cycles, *Uromyces Pisi* etc.

The peridium of this species is more strongly developed than that of the following one; its cells are densely warted, and arranged in distinct rows. A long account of the behaviour of the parasite is given by Plowright (*l.c.*). The spores germinate readily in the summer as soon as produced.

DISTRIBUTION: Europe.

2. *Endophyllum Sempervivi* De Bary.

Uredo Sempervivi A. et S. Consp. p. 126.

Endophyllum Sempervivi De Bary, Morphol. p. 304 (sec. Saccardo).

Cooke, Handb. p. 546; Micr. Fung. p. 200.

Plowr. Ured. p. 229. Sacc. Syll. vii. 767.

Fischer, Ured. Schweiz, p. 436, f. 297.

Hoffmann, Centralbl. f. Bakter. xxxii. 137, f. 1—14 and pl. i, ii.

Spermogones. Scattered amongst the æcidia, roundish.

Teleutospores. Sori rather large, amphigenous, sunken in the leaf, æcidium-like, surrounded by many layers of hyphæ and by a peridium, which opens by a pore at the summit and finally becomes cup-shaped; spores bluntly polygonal or roundish, yellowish-brown, densely reticulate-verrucose, $24-35 \times 21-28 \mu$; epispore $3-4 \mu$ thick.

On *Sempervivum tectorum*; also found on *S. calcareum*, *S. globiferum*, *S. montanum* (Plowright), *S. arachnoideum* (Fischer) and others (Saccardo). Not common, Warwickshire, Forden, Kew Gardens, etc. April—August. (Figs. 252, 253.)

It has been proved by De Bary, Hoffmann and others that the basidiospores produced by the teleutospores infect the leaves, and from them arises a mycelium which perennates in the stem. It produces spermogones and teleutospores in the following spring. The affected leaves are more erect than normal ones, twice as long, narrower and yellowish at the base: infested plants should be burnt, so that they may not infect others. See the fuller account given on pp. 53-5.

DISTRIBUTION: Europe.



Fig. 252. *E. Sempervivi*. Sori on *Sempervivum montanum* (reduced).



Fig. 253. *E. Sempervivi*. Æcidio-teleutospore germinating (after Hoffmann).

MELAMPSORACEÆ

Teleutospores not pedicellate, but seated on a dilated hyphal cell, produced singly in the tissues of the host or compacted side by side into flat crusts, one-celled or divided longitudinally into 2—4 cells. Germination by an external basidium, with minute round basidiospores (about $10\ \mu$). Uredospores abstricted singly. Uredo-sori and æcidia with or without a peridium.

		<i>Melampsora.</i>
		<i>Melampsoridium.</i>
MELAMPSOREÆ.	Teleutospores brown or brownish, on Seed-plants.	<i>Melampsorella.</i>
		<i>Pucciniastrum.</i>
		<i>Thecopsisora.</i>
		<i>Calyptospora.</i>
		<i>Hyalopsisora.</i>
HYALOPSOREÆ.	Teleutospores hyaline, on Ferns.	<i>Milesina.</i>
		<i>Uredinopsis.</i>

MELAMPSORA Cast.

Heterœcious, or in a few species autœcious. The sori, of all kinds, may be subcuticular or subepidermal. Teleutospores one-celled, rarely septate, compacted laterally into flat, irregular, dark-coloured crusts; wall coloured, smooth. Uredospores not enclosed in a peridium, abstricted singly, without evident germ-pores, intermixed with capitate paraphyses. Æcidia of the œcema-type, pulvinate, without peridium and generally without paraphyses. Spermatogones, shallow, hemispherical, without ostiolar filaments.

There are seven species of *Melampsora* recorded for North America, but only one of these, *M. Lini*, is found in Britain, and one other, *M. alpina* on arctic and alpine species of *Saxifraga* and *Salix*, in Europe. The *Melampsoras* on *Salix* and *Populus* form a very complex group; this is no doubt correlated with the fact that the genera *Salix* and (to a smaller extent) *Populus* are themselves in a state of flux, evolving many closely related species and possessing many

hybrids. Klebahn is the author who has chiefly studied the group, and the following account of the known or supposed British species on *Salix* is mainly founded upon his work.

The artificial key to the species, here given, is based upon that of Fischer, but must be taken with a little reservation since, as is now known, the life-histories of such heterœcious forms require to be worked out for each country separately.

HETERœCIOUS.

A. Teleutospores on *Salix*.

- a. Uredospores oblong, smooth at upper end. Cæoma on *Allium*.
 1. Teleutospores subepidermal. *M. Allii-Salicis-albae*.
 2. Teleutospores subcuticular. *M. Allii-fragilis*.
- b. Uredospores roundish, without smooth spot.
 1. Teleutospores subcuticular, strongly thickened above, with a conspicuous germ-pore. Cæoma on *Larix*.
M. Larici-Caprearum.
 2. Teleutospores not strongly thickened above, without an evident germ-pore.
 - (1) Teleutospores subepidermal.
Cæoma on *Larix*. *M. Larici-epitea*.
 „ on Orchidaceæ. *M. Orchidi-repentis*.
 „ on *Euonymus*. *M. Euonymi-Caprearum*.
 „ on *Ribes*. *M. Ribesii-purpureae*.
 - (2) Teleutospores subcuticular. *M. Ribesii-viminalis*.

B. Teleutospores on *Populus*.

- a. Uredospores elongated, smooth above. Teleutospores on *P. nigra*, *P. balsamifera*.
 1. Cæoma on *Larix*. Teleutospores epiphyllous.
M. Larici-populina.
 2. Cæoma on *Allium*. Teleutospores hypophyllous.
M. Allii-populina.
- b. Uredospores roundish, not smooth above. Teleutospores on *P. alba*, *P. tremula*.
 1. Cæoma on *Larix*. *M. Larici-tremulae*.
 2. „ on *Pinus*. *M. pinitorqua*.
 3. „ on *Mercurialis*. *M. Rostrupii*.

AUTœCIOUS.

Teleutospores not on Salicaceæ.

M. Hypericorum, *M. Lini*, *M. Euphorbiae*, *M. vernalis*.

1. **Melampsora Larici-Caprearum** Kleb.

Caeoma Larici Plowr. Ured. p. 262 p.p.

Melampsora salicina Lév. ; Cooke, Handb. p. 522 ; Micr. Fung. p. 219.

M. farinosa Schröt. Flor. Schles. iv. 360. Plowr. Ured. p. 238 p.p.
(see note).

M. Larici-Caprearum Kleb. in Forstl.-naturw. Zeitschr. 1897, p. 469.
Fischer, Ured. Schweiz, p. 483, f. 312.

Æcidiospores. Cæomata minute, pale-orange; spores roundish, oblong, or polygonal, $15-25 \times 12-17 \mu$; epispore up to 2μ thick, finely verruculose, with many thin places (? germ-pores).

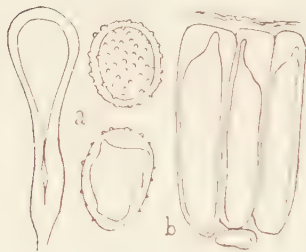


Fig. 254. *M. Larici-Caprearum*. Paraphysis and uredospores (one showing the thin places in the epispore); b, telentospores. On *S. Caprea*.



Fig. 255. *M. Larici-Caprearum*. Teleuto-sori, on upper face of leaf of *S. Caprea*, nat. size; teleuto-spore, germinating, $\times 360$.

Uredospores. Sori hypophyllous, showing as yellow spots on the upper side, variable in size and arrangement, 1—3 mm. wide; spores roundish, oval, or polygonal, $14-21 \times 13-15 \mu$; epispore $2-2\frac{1}{2} \mu$ thick, firm, distantly echinulate, with thin places (? germ-pores); paraphyses capitate, $50-60 \times 18-26 \mu$, thickened (up to 5μ) above.

Teleutospores. Sori epiphyllous, 1 mm. or more wide, dark reddish-brown, frequently confluent in extensive crusts, lying between the cuticle and the epidermis; spores prismatic, rounded below, $30-45 \times 7-14 \mu$, rather unequal in length; epispore clear-brown, thin (1μ), but thickened (up to 10μ)

above where it is pierced by an evident laterally placed germ-pore.

Cæomata on *Larix europaea*; uredo- and teleutospores on *Salix Caprea*, more rarely on *S. aurita* and other *Salices*. The commonest species. (Figs. 254, 255.)

The teleutospores germinate the following spring. They are distinguished from those of all the allied species by being thickened above. Plowright remarks that the cæoma is not uncommon early in the year on Larch foliage, but is very inconspicuous and easily overlooked; he found the æcidiospores, in company with the uredospores on *S. Caprea*, at West Malvern, June, 1900. But it is almost impossible to say, without experiment, to which form of *Melampsora* any given cæoma on Larch is to be assigned.

Plowright's *M. farinosa* seems to be chiefly this species, but several of the allied forms are continually recorded under the same name. The reddish teleuto-sori on the upper side of the leaf, are distinctive and are easily found by looking for them from September onwards. It may be mentioned here that both uredo- and teleutospores of the *Melampsoras* on Willow and Poplar germinate readily: if the germinating uredospores are placed upon healthy leaves and kept in a damp chamber, infection usually follows in 7—10 days.

2. *Melampsora Euonymi-Caprearum* Kleb.

Uredo confluens var. *Euonymi* Mart. Flor. Mosq. p. 230. Cooke, Handb. p. 527.

U. Euonymi Cooke, Micr. Fung. p. 216.

Cæoma Euonymi Plowr. Ured. p. 260.

Melampsora Euonymi-Caprearum Kleb. in Pringsh. Jahrb. f. Wissensch. Bot. 1900, xxxiv. 358. Fischer, Ured. Schweiz, p. 489.

Spermogones. Flatly pulvinate.

Æcidiospores. Cæomata mostly hypophyllous, bright-orange, in elongated clusters on orange spots, $\frac{1}{2}$ —1 mm. diam.; spores oval, rarely oblong, $18\text{--}23 \times 14\text{--}19 \mu$; episore thick (up to 5μ), finely and densely verrucose.

Uredospores. Sori hypophyllous, on discoloured spots which show distinctly on the upper side, small, $\frac{1}{2}$ mm. wide, pulvinate, single or in groups; spores mostly roundish, orange, $14\text{--}19 \times 14\text{--}17 \mu$, distantly echinulate without smooth spots; episore thin, or at times thickened (up to 4μ), with several germ-

pores: paraphyses capitate with a slender pedicel, thickened (up to $8\ \mu$) above, $50-70 \times 18-25\ \mu$.



Fig. 256. *M. Euonymi-Caprearum*. Old dead leaf of *S. Caprea*, showing teleuto-sori on lower face (slightly reduced).

Teleutospores. Sori hypophyllous, covered by the epidermis, small, about $\frac{1}{2}$ mm. diam., but united into groups bounded by the veins, brown with a tinge of bluish-grey; spots brown on the upper surface; spores irregularly prismatic, rounded at both ends, $25-40 \times 7-13\ \mu$; epispore thin, clear-brown, scarcely thickened above, with a barely perceptible apical germ-pore.

Cæomata on *Euonymus europæus*, August, September, rather rare; uredo- and teleutospores on *Salix aurita*, *S. Caprea*, *S. cinerea*. (Fig. 256.)

Fischer records the cæoma in Switzerland in May and June. The distinction of this species from the preceding one (apart from the æcidial host) lies in the teleuto-sori; these are hypophyllous and subepidermal, while those of *M. Larici-Caprearum* are epiphyllous and subcuticular. It is not certain, however, that this distinction is absolute; Fischer in a culture on *S. cinerea* obtained a few teleuto-sori showing also the latter characters. There is a further difference in the form of the teleutospores.

3. *Melampsora Larici-epitea* Kleb. (emend. Fischer).

Uredo epitea K. et S. Mycol. Heft. i. 68.

Lecythæa epitea Lév.; Cooke, Micr. Fung. p. 221.

Melampsora epitea Thüm.; Plowr. Ured. p. 239.

M. Larici-epitea Fischer, Ured. Schweiz, p. 485, f. 313. Kleb. in Zeitschr. f. Pflanzenkr. 1899, ix. 88.

Æcidiospores. Cæomata hypophyllous, scattered or in rows, with yellow spots on the upper surface, roundish or oblong, $\frac{1}{2}-1\frac{1}{2}$ mm. long, pale orange-yellow; spores roundish or somewhat polygonal, finely warted, $15-25 \times 10-21\ \mu$; epispore $1\frac{1}{2}-3\ \mu$ thick, with no recognisable germ-pores.

Uredospores. Sori amphigenous, seated on yellow spots, orange-yellow, $\frac{1}{4}-1\frac{1}{2}$ mm. diam.; spores mostly oval, sometimes oblong, roundish, or angular, echinulate, orange, $12-25 \times 9-$

19 μ ; epis pore $1\frac{1}{2}$ — $3\frac{1}{2}$ μ thick, without perceptible germ-pores; paraphyses capitate, with a thin pedicel, occasionally clavate, thickened (up to 10 μ) above, hyaline, 35 — 80×15 — 24 μ .



Fig. 257. *M. Larici-epitea*.
Cæoma on Larch leaf, $\times 2$
(one of Plowright's cultures
from *S. cinerea*).



Fig. 258. *M. Larici-epitea*.
Uredospores and para-
physes, on *S. viminalis*.

Teleutospores. Sori amphigenous, covered by the epidermis, at length dark-brown, sometimes tinged round with greyish-blue or violet, $\frac{1}{4}$ —1 mm. diam., densely clustered or confluent; spores prismatic or subclavate, rounded at both ends, occasionally narrowed above, 20 — 50×7 — 14 μ ; epis pore clear-brown, uniformly thin, without an evident germ-pore.

Cæomata on *Larix europaea*; uredo- and teleutospores on many species of *Salix*. The teleutospores in October and November. (Figs. 257, 258.)

This species is one of the most complex of all the Melampsoraceæ; it has been divided into about eight biological races, all of which have their cæoma on Larch, while the other spore-forms are specialised to certain species of Willow. It is recorded on the following British *Salices* for other countries, but it is not possible as yet to say on which of these it is found in this country: *S. aurita*, *Caprea*, *cinerea*, *fragilis*, *Smithiana*, *viminalis* for the typical form; *nigricans* for the form *M. Larici-nigricantis* Schneider; *purpurea* for the form *M. Larici-purpureae* Schneider; and *reticulata* for *M. Larici-reticulatae* Schneider. Morphological differences between these forms are not discoverable.

The teleutospores germinate in the spring following after their formation. The teleuto-sori are formed under the epidermis, and appear to start usually just below a stoma; they often occupy entire areas bounded by the veins. This description is taken mainly from Fischer. The teleutospores are distinguished from those of *M. Larici-Caprearum* by the total want of thickening at the apex. Plowright produced the cæoma on Larch from the teleutospores on *Salix cinerea*, May 24th, 1900.

4. **Melampsora Ribesii-viminalis** Kleb.

Caeoma Ribesii Link, Sp. Pl. ii. 28 p.p.

Melampsora Ribesii-viminalis Kleb. in Pringsh. Jahrb. f. Wissensch. Bot. 1900, xxxiv. 363. Fischer, Ured. Schweiz, p. 494.

Spermogones. Pulvinate, with flat hymenium.

Aecidiospores. Caeomata hypophyllous, on discoloured spots which show on both sides, arranged in groups, 1.5 mm. wide, bright-orange: spores roundish, rarely oval, $18-23 \times 14-17 \mu$; epispore $2-4 \mu$ thick, with many thinner places (2 germ-pores), finely and densely verruculose.

Uredospores. Sori hypophyllous, minute, about $\frac{1}{4}$ mm., scattered or in groups, pale orange-yellow: spores more or less round, $15-19 \times 14-16 \mu$; epispore 2μ thick, uniformly echinulate: paraphyses capitate or more often clavate, hardly thickened above, $50-70 \times 18-25 \mu$.

Teleutospores. Sori epiphyllous, developed between the cuticle and the epidermis, $\frac{1}{4}-\frac{1}{2}$ mm., scattered or in groups over the whole leaf, dark-brown, shining; spores prismatic, rounded at both ends, more or less irregular, $25-40 \times 7-14 \mu$; epispore thin, clear-brown, not thickened above, with no evident germ-pore.

Caeomata on *Ribes Grossularia*, *R. nigrum*, *R. rubrum*; uredo- and teleutospores on *Salix viminalis*.

Klebahn showed, by many trials, the genetic connection of the parasites on these species. The teleutospores can be distinguished from all others except those of *M. Larici-Caprearum* and *M. Allii-Galanthi-fragilis* by their being subcuticular. *M. Larici-epitea* is also recorded for *Salix viminalis*, but that has its teleutospores subepidermal, and the paraphyses of the uredo-sori strongly thickened at the apex. The caeoma on *Ribes* does not seem to be recorded for this country and is apparently rare.

5. **Melampsora Ribesii-purpureae** Kleb.

Melampsora Ribesii-purpureae Kleb. in Pringsh. Jahrb. f. Wissensch. Bot. 1901, xxxv. 667. Fischer, Ured. Schweiz, p. 492.

Spermogones. Subconical, with flat hymenium.

Aecidiospores. Caeomata mostly hypophyllous, on pale-yellow spots which show on both sides, scattered or in subcircinate groups, $\frac{1}{2}-1\frac{1}{2}$ mm., sometimes confluent, surrounded by the

torn epidermis, orange: spores roundish or subpolygonal, $18-20 \times 15-18 \mu$; epispore about 3μ thick, finely and densely verruculose, with a few thinner places (? germ-pores).

Uredospores. Sori mostly hypophyllous, on conspicuous bright-yellow spots which show on both sides, $\frac{1}{2}-1\frac{1}{2}$ mm., pulvinate, surrounded by the torn epidermis, bright orange-red; spores roundish, uniformly but not densely echinulate, $15-23 \times 14-19 \mu$; epispore up to $2\frac{1}{2} \mu$ thick, with a few thinner places; paraphyses variable, capitate or clavate, $40-70 \times 12-21 \mu$, not thickened above.

Teleutospores. Sori amphigenous, but mostly hypophyllous, scattered or in little groups over the whole surface, subepidermal, small, $\frac{1}{4}-\frac{1}{2}$ mm. diam., brownish-black; spores irregular, prismatic, rounded at both ends, $25-35 \times 7-10 \mu$; epispore thin, clear-brown, not thickened above, without evident germ-pore.

Cæomata on *Ribes alpinum*, *R. Grossularia* (not on *R. nigrum*, *R. rubrum*); uredo- and teleutospores on *Salix purpurea*.

Description according to Fischer; Klebahn's experiments have demonstrated the connection of the parasites on these hosts. It is probable that *M. Ribesii-auritae* Kleb. is only a biological race of the same fungus, having spermogones and cæoma-spores (according to Klebahn) on *Ribes nigrum* as well as on the two mentioned above, and its other spore-forms on *Salix aurita* and possibly *S. Caprea*. They are scarcely distinguishable, if at all, morphologically; both may be British.

M. Larici-epitea is also recorded on *S. purpurea*, but can be distinguished by its densely clustered teleuto-sori on spots often bounded by veins, and the paraphyses of the uredo-sori strongly thickened above. *M. mixta* (Plowr. Ured. p. 239) may belong to either, but his species extended to the branches and inflorescence.

6. *Melampsora Orchidi-repentis* Kleb.

Uredo confluens var. *Orchidis* A. et S. Consp. p. 122. Cooke, Handb. p. 527.

U. Orchidis Mart. Flor. Mosq. p. 229. Cooke, Micr. Fung. p. 216.

Cæoma Orchidis Wint. Pilze, p. 256. Plowr. Ured. p. 261; Gard. Chron. 1890, viii. 41. Sacc. Syll. vii. 868.

Melampsora Orchidi-repentis Kleb. in Pringsh. Jahrb. f. Wissensch. Bot. 1900, xxxiv. 369. Fischer, Ured. Schweiz, p. 488.

Spermogones. Hardly projecting, flat, mostly under the stomata.

Æcidiospores. Cæomata irregular in outline, clustered or circinate on large pale-yellowish spots, often confluent, 1—2 mm. diam.; bright orange-yellow; spores roundish-polygonal, $11\text{--}20 \times 11\text{--}15 \mu$; epispore very thin, delicately warted.



Fig. 259. *M. Orchidirepentis*. Cæoma on leaf of *Listera ovata*, from one of Plowright's cultures (reduced).

Uredospores. Sori hypophyllous, minute, deep-orange, causing yellow spots on the upper side; spores more or less round, orange, echinulate, $13\text{--}17 \times 12\text{--}14 \mu$; paraphyses mostly capitate, with thin pedicels, $40\text{--}70 \times 16\text{--}20 \mu$.

Teleutospores. Sori hypophyllous or a few on the upper side, subepidermal, small, dark-brown; spores prismatic, rounded at both ends, $16\text{--}48 \times 7\text{--}14 \mu$; epispore clear-brown, uniformly thin (about 1μ), without any evident germ-pore.

Cæomata on *Listera ovata*, *Orchis latifolia*, *O. maculata*, May, June; uredo- and teleutospores on *Salix aurita*, *S. repens*. Not common. (Fig. 259.)

The cæoma is also recorded on *Listera cordata*, *Goodyera repens*, and *Gymnadenia conopsea*, but no experimental proof of the connection seems to be forthcoming in the case of these species, though both Plowright and Klebahn have demonstrated it for the other species. The teleutospores germinate, as usual, after the winter's rest. Soppitt found the cæoma on *O. maculata* and the teleutospores on *S. repens* growing together near Southport.—The æcidium of *Puccinia Orchidearum-Phalaridis* can be readily distinguished from the cæoma of this species by its evident peridium and the regularity of its form.

7. *Melampsora Allii-fragilis* Kleb.

Uredo Alliorum DC.; Cooke, Mier. Fung. p. 217 p.p.

Cæoma Alliorum Link; Plowr. Ured. p. 261 p.p.

Melampsora Vitellinae Plowr. l.c. p. 240 p.p.

M. Allii-fragilis Kleb. in Pringsh. Jahrb. f. Wissensch. Bot. 1901, xxxv. 671. Fischer, Ured. Schweiz, p. 481.

Spermogones. Scarcely projecting, with flat hymenium.

Æcidiospores. Cæomata on the leaves and stems, also on the bulbils, clustered on discoloured spots, usually oblong, up to 2 mm. long, surrounded by the torn epidermis, bright orange-yellow; spores irregular, mostly polygonal, seldom round, $18-25 \times 12-19 \mu$; epispore $1-1\frac{1}{2} \mu$ thick, finely verruculose.

Uredospores. Sori hypophyllous or partly epiphyllous, minute, $\frac{1}{2}$ mm., circular, surrounded by the torn epidermis, reddish-orange, causing reddish-yellow spots on the upper side; spores distinctly oblong or obovate, $22-33 \times 13-15 \mu$; epispore up to 3μ thick, with thinner places (? germ-pores), distantly echinulate, but smooth and somewhat thinner above; paraphyses capitate or clavate, $50-70 \times 15-20 \mu$, with thin pedicel and uniformly thickened membrane ($3-5 \mu$).

Teleutospores. Sori chiefly epiphyllous, between the cuticle and the epidermis, scattered or in groups, pulvinate, $\frac{1}{4}-1\frac{1}{2}$ mm. broad, dark-brown, shining; spores prismatic, rounded at both ends, $30-48 \times 7-14 \mu$; epispore clear-brown, uniformly thick (about 1μ), without evident germ-pore; basidiospores orange.

Cæomata on *Allium Cepa*, *A. ursinum* and others; uredo- and teleutospores on *Salix fragilis*, *S. pentandra*, and the hybrid between them.

The teleutospores germinate after a winter's rest. Klebahn's *M. Galanthi-fragilis* is morphologically identical, even occurring on the same species of *Salix*, but has its cæomata on *Galanthus nivalis*; it can only be considered as a biological race. The same author's *M. Larici-pentandrae* infests the same species of *Salix*, but has its cæomata on *Larix*; it is distinguished, however, by its teleuto-sori, which occur on both sides of the leaves, are more minute (though often confluent) and arise below the epidermis. I have a *Melampsora* on *Salix fragilis*, which has minute teleuto-sori abundantly on the upper surface and beneath the epidermis. This might belong to *M. Larici-pentandrae* Kleb.

8. *Melampsora Allii-Salicis-albæ* Kleb.

Melampsora Allii-Salicis-albæ Kleb. in Zeitschr. f. Pflanzenkr. 1902, xii. 19. Fischer, Ured. Schweiz, p. 480.

Spermogones. Rather flat.

Æcidiospores. Cæomata on the leaves and stems, in groups

on yellowish spots, about 1 mm. diam., surrounded by the epidermis, bright orange-yellow; spores mostly roundish, $17-26 \times 15-18 \mu$, densely verruculose.

Uredospores. Sori of two kinds: (1) in summer and autumn on the leaves, hypophyllous, $\frac{1}{2}$ mm. wide, on inconspicuous discoloured spots, (2) in spring, erumpent from the bark of young twigs and as much as 5 mm. long, afterwards on the young leaves, as much as 2 mm. long and densely crowded; spores all similar, distinctly oblong, sometimes clavate or pyriform, $20-36 \times 11-17 \mu$; epispore 2μ thick, smooth above, distantly echinulate below; paraphyses capitate, $50-70 \times 15-20 \mu$, not thickened above, absent from the cortical sori.

Teleutospores. Sori amphigenous, subepidermal, scattered thinly over the leaf-surface singly or in groups, dark-brown; spores prismatic, rounded at both ends, clear-brown, $25-45 \times 7-10 \mu$; epispore scarcely 1μ thick, not thickened above, without evident germ-pore.

Æcidia on *Allium ursinum* and other species; uredo- and teleutospores on *Salix alba*.

The caëma on *Allium* is indistinguishable from that of *M. Allii-fragilis* or *M. Allii-populina*. This species can winter by its teleutospores which produce the caëma on *Allium*, or by the perennial mycelium in the cortex of the branches on which the uredospores appear in spring *before* the caëma is produced; these sori are without paraphyses. The whole of this account is due to Klebahn: I have a specimen from Yorkshire (C. Crossland) which is referred, doubtfully, to this species.

9. *Melampsora arctica* Rostr.

M. arctica Rostr. Fung. Groenland. 1888, p. 535. Sacc. Syll. Fung. vii. 595. Annals of Scott. Nat. Hist. 1911, p. 37.

Uredospores. Sori hypophyllous, gregarious, yellow; spores spheroid to ovoid, echinulate, $18-23 \mu$; paraphyses clavate.

Teleutospores. Sori hypophyllous, scattered, very small, dark-brown; spores prismatic, reddish-brown.

On leaves of *Salix herbacea*, Scotland, Ben-an-Dothaidh, at 3100 ft. (J. A. Wheldon and A. Wilson).

Plants of the *Salix* were brought from Scotland and cultivated at Walton, near Liverpool; there were then uredospores only. When the leaves fell, they were left on the ground, and two telento-sori were developed on them, of a rufous black colour. I have not seen the specimens.

10. *Melampsora populina* Lév.

Melampsora populina Lév. Ann. Sci. Nat. 1847, p. 375. Cooke, Handb. p. 523; Micr. Fung. p. 219. Plowr. Ured. p. 242. Sacc. Syll. vii. 590.

(1) MELAMPSORA ALLII-POPULINA Kleb.

Caecoma Alliorum Link; Plowr. Ured. p. 261 p.p.

M. populina Cooke, Micr. Fung. pl. 9, f. 195, 196.

Melampsora Allii-populina Kleb. in Zeitschr. f. Pflanzenkr. 1902, xii. 25. Fischer, Ured. Schweiz, p. 504.

Spermogones. Pulvinate, projecting.

Æcidiospores. Caemata about 1 mm. wide, mostly in groups on yellowish-white spots on the leaves, surrounded by the epidermis, bright orange-red; spores roundish or oval or polygonal, $17-23 \times 14-19 \mu$; episore about 2μ thick, but sometimes thicker and then obviously thin at certain spots (? germ-pores), verruculose.

Uredospores. Sori hypophyllous, or even rarely epiphyllous, round, scarcely 1 mm. wide, surrounded by the epidermis, causing yellowish spots, bright reddish-orange; spores distinctly

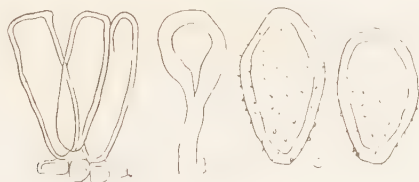


Fig. 260. *M. Allii-populina*. a, teleutospores; b, paraphysis; c, uredospores. On *Populus nigra*.

oblong or clavate, rarely oval, $24-38 \times 11-18 \mu$; episore $2-4 \mu$ thick, with sunken places (? germ-pores), sometimes thicker at one end, but without any equatorial thickening, distantly echinulate, but smooth above; paraphyses mostly capitate, $50-60 \times 14-22 \mu$, with a wall uniformly $2-3 \mu$ thick.

Teleutospores. Sori hypophyllous, subepidermal, scattered over the leaf singly and in groups, pulvinate, $\frac{1}{4}$ — $\frac{3}{4}$ mm., blackish-brown, not shining; spores prismatic, rounded at both ends, $35\text{--}60 \times 6\text{--}10 \mu$; episore clear-brown, $1\text{--}1\frac{1}{2} \mu$ thick, scarcely thickened above, without evident germ-pore.

Cæomata on *Allium Cepa*, *A. ursinum* and other species, May: uredo- and teleutospores on *Populus nigra*, *P. balsamifera*. (Fig. 260.)

The description is chiefly after Klebahn. The teleutospores mature in February of the following year; I find them shorter than given above, viz. $25\text{--}32 \mu$, and somewhat truncate at the summit. The cæoma of species of *Melampsora* on *Allium* is easily distinguished from the æcidium of *Puccinia Winteriana* on the same host by the absence of a peridium.

(2) MELAMPSORA LARICI-POPULINA Kleb.

Cæoma Laricis Plowr. Ured. p. 262 p.p.

Melampsora populina Lév.; Plowr. Ured. p. 242 p.p. (see note, "Biology," p. 243).

M. Larici-populina Kleb. in Zeitschr. f. Pflanzenkr. 1902, xii. 43. Fischer, Ured. Schweiz, p. 502, f. 316.

Æcidiospores. Cæomata on hardly perceptible spots, scarcely 1 mm. long, bright yellowish-orange; spores oval or roundish, $17\text{--}22 \times 14\text{--}18 \mu$; episore $1\frac{1}{2}\text{--}2 \mu$ thick, colourless, finely verruculose.

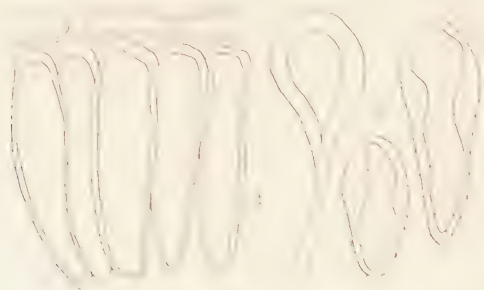


Fig. 261. *M. Larici-populina*. a, teleutospores; b, uredospores and paraphysis. On *P. ontariensis*.

Uredospores. Sori mostly hypophyllous, in little groups, causing yellowish angular spots on the upper side, rarely

solitary and epiphyllous, up to 1 mm. wide, at first covered by the raised epidermis and a layer of hyphæ, at length uncovered and surrounded by the same, distributed over the whole leaf-surface; spores distinctly oblong, $30-40 \times 13-17 \mu$; epispore about 2μ thick, at the equator thickened up to $5-6 \mu$, covered with rather distant spines except at the summit which is smooth; paraphyses clavate-capitate, $40-70 \times 14-18 \mu$, strongly thickened (up to 10μ) above.

Teleutospores. Sori epiphyllous, minute but united in groups and confluent, distributed over nearly the whole leaf, covered by the epidermis, clear translucent-brown, then red-brown, and at length black; spores prismatic, rounded above and less so below, $40-50$ or more $\times 7-10 \mu$; epispore pale, scarcely 1μ thick, but reaching $2\frac{1}{2}-3 \mu$ above where it is faintly coloured and without evident germ-pore.

Cæomata on *Larix europæa*; uredo- and teleutospores on *Populus balsamifera* (*ontariensis*), *P. canadensis*, *P. nigra*, *P. pyramidalis* (*italica*), and also on other species, in September and October. Not uncommon. (Fig. 261.)

The description of the cæomata is after Klebahn. This species is distinguished from *M. Allii-populina* by the following points: the elongated uredospores have a distinct equatorial thickening or rather swelling; the teleuto-sori are epiphyllous, and the spores are very slightly thickened at the summit. On *P. ontariensis* I have seen the teleuto-sori so thick and crisp as to remind one of *Phyllachora Ulmi* on elm-leaves.

11. *Melampsora Tremulæ* Tul.

Melampsora Tremulæ Tul. Ann. Sci. Nat. 1854, p. 95. Cooke, Handb. p. 522; Micr. Fung. p. 219. Plowr. Ured. p. 240. Sacc. Syll. vii. 589.

(1) *MELAMPSORA LARICI-TREMULÆ* Kleb.

Cæoma Laricis Plowr. Ured. p. 262 p.p.

Melampsora Larici-tremulæ Kleb. in Forstlich.-naturwiss. Zeitschr. 1897, p. 468. Fischer, Ured. Schweiz, p. 498, f. 315.

Æcidiospores. Cæomata solitary or in little groups, on yellowish spots, minute, scarcely 1 mm. diam., pale-orange or flesh-colour; spores roundish, oval or polygonal, $14-17 \times 12-16 \mu$; epispore about 1μ thick, verruculose.

Uredospores. Sori hypophyllous, minute, $\frac{1}{2}$ mm., somewhat pulvinate, pulverulent, spots obsolete; spores oval, oblong or obovate, rarely round, $15-22 \times 10-15 \mu$; epispore about 2μ thick, covered with stout spines; paraphyses distributed throughout the sorus, elongated-clavate rather than capitate, $40-45 \times 8-17 \mu$, with a thick wall ($3-9 \mu$).

Teleutospores. Sori hypophyllous, minute, $\frac{1}{2}-1$ mm. diam., covered by the epidermis, dark-brown; spores prismatic, rounded at both ends, $40-60 \times 7-12 \mu$; epispore thin ($1-2 \mu$), not thickened above, with a scarcely evident germ-pore.

Cæomata on *Larix europaea*; uredo- and teleutospores on *Populus alba*, *P. tremula*, rarely *P. balsamifera*, September, October.

The description is after Klebahn. The teleutospores germinate after a winter's rest. Though Plowright records that he could obtain no result "by placing the germinating teleutospores of *M. tremulae* on young larch trees" (*l.c.* p. 241), the truth of the heteroecism has been abundantly demonstrated by Hartig, Klebahn and Fischer. Plowright mentions that Prof. Trail had found these two forms growing in company near Aberdeen; and the meaning of his failure is simply that he was using one of the other *Melampsorae* that grow on *P. tremula*. It has been suggested, but not proved, that *M. pinitorqua* is itself only a biological race, and there are also *M. Magnusiana* (Klebahn), and *M. Rostrupii* which may come under the same category; see p. 353.

(2) MELAMPSORA PINITORQUA Rostr.

Cæoma pinitorquum A. Braun, in Monatsb. Berl. Akad. 1863, p. 624.

Melampsora pinitorqua Rostr. Tidsskr. f. Skovbrug, 1889, xii. 177.

Fischer, Ured. Schweiz, p. 499. Yorkshire Fungus Flora, p. 183.

Massee, Text-book of Fungi, f. 22, 98; Text-book of Plant Diseases, p. 235, f. 60; Dis. Cultiv. Plants, p. 325, f. 98.

Æcidiospores. Cæomata erumpent through the cortex of young shoots, solitary, linear, reaching 20×3 mm., reddish-orange; spores roundish or oval, pale reddish-yellow, $14-20 \times 13-17 \mu$, or oblong, $22 \times 10 \mu$; epispore about 2μ thick, delicately verruculose.

Uredospores. Sori hypophyllous, on spots which show yellow chiefly on the upper side, solitary or in groups, often scattered over the whole surface, scarcely $\frac{1}{2}$ mm. wide, pulvinate; spores

oval to ovate-oblong, $15-22 \times 11-16 \mu$; epispore uniformly about 2μ thick, with two germ-pores(?), echinulate all over; paraphyses distributed throughout the sorus, clavate, not capitate, $40-50 \times 12-17 \mu$, with a uniformly thick wall ($3-7 \mu$).

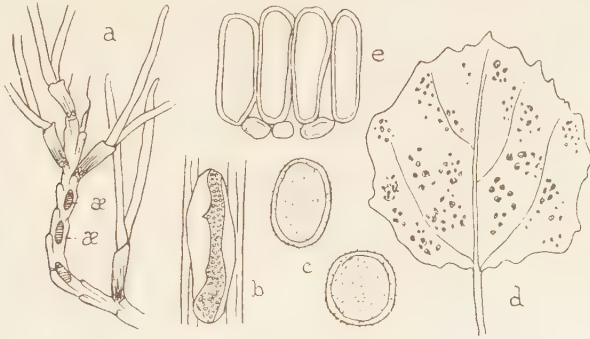


Fig. 262. *M. pinitorqua* (from a German specimen, ex herb. Sydow). *a*, a young shoot of Pine, in June, with newly-formed leaves, showing three caemata (*ae*), shaded; the leaves have been removed from the affected portion, which is beginning to be curved; *b*, a caema, $\times 10$; *c*, aecidiospores; *d*, old leaf of Aspen, showing numerous teleuto-sori on the lower surface; *e*, teleutospores.

Teleutospores. Sori hypophyllous, mostly in clusters, about $\frac{1}{2}$ mm. wide, covered by the epidermis, crust-like, brown, not shining; spores prismatic, rounded at both ends, $20-35 \times 7-11 \mu$; epispore pale-brownish, scarcely 1μ thick, not thickened above, without evident germ-pore.

Caemata on young shoots of *Pinus silvestris* which they distort, May, June; uredo- and teleutospores on *Populus alba*, *P. tremula*, and their hybrid (*P. canescens*), not on *P. balsamifera*. Rare in this country. (Fig. 262.)

The connection of the forms on the two hosts was first demonstrated by Rostrup and confirmed by Hartig and Klebahn. See p. 57.

(3) MELAMPSORA ROSTRUPII Wagner.

Uredo confluens DC.; Cooke, Handb. p. 527; Mier. Fung. p. 216, pl. 7, f. 133, 134.

Caecoma Mercurialis Link; Plowr. Ured. p. 260. Sacc. Syll. vii. 868.

Melampsora aecidioides Plowr. Ured. p. 241. Sacc. Syll. vii. 590.

M. Rostrupii Wagner, in Oester. Bot. Zeitschr. 1896, xlv. 273
Fischer, Ured. Schweiz, p. 501.

Spermogones. Epiphyllous, or a few hypophyllous, in large round clusters, honey-coloured.

Æcidiospores. Cæomata hypophyllous and on the petioles and stems, in clusters on pale-yellow spots, often circinate round the spermogones, about 1 mm. wide, often confluent in patches 1—1½ cm. wide, bright-orange; spores roundish-polygonal or oval, 13—18 × 12—16 μ ; episporium 1—1½ μ thick, finely and densely verruculose.

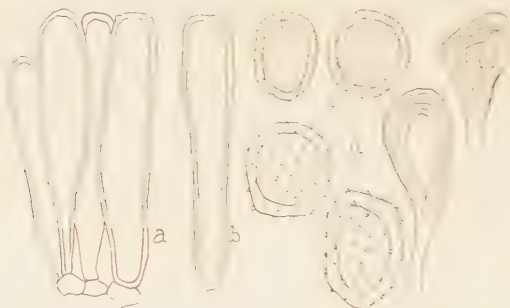


Fig. 263. *M. Rostrupii*. a, teleutospores on *P. tremula*; b, teleutospore on *P. alba*; c, æcidiospores on *Mercurialis perennis*; d, paraphyses and uredospores on *P. tremula* (one paraphysis contains the orange remains of the protoplasm).

Uredospores. Sori hypophyllous, about 1 mm. wide, pulvinate, compact, causing large yellow spots on both sides: spores oval or sometimes roundish-polygonal, 21—25 × 14—18 μ ; episporium up to 3 μ thick, covered with stout rather distant spines; paraphyses distributed throughout the sorus, clavate or somewhat capitate, 50 × 15—23 μ , with a thick wall (3—6 μ).

Teleutospores. Sori hypophyllous, ½—1 mm. wide, scattered over the whole leaf, covered by the epidermis, dark-brown; spores prismatic, rounded at both ends, pale-brown, 40—55 × 8—10 μ ; episporium thin (1—2 μ), not thickened above, without any evident germ-pore.

Cæomata on *Mercurialis perennis*, April—June; uredo- and teleutospores on *Populus alba*, *P. tremula*, and occasionally on other species, September and October. (Fig. 263.)

The connection of the two forms has been shown by Rostrup, Nielsen, Plowright, Klebahn, Wagner, and Jacky. The teleutospores may be found

by looking in spring on fallen leaves of *P. tremula*, *P. alba*, at places where *Mercurialis* is found to be affected. The caëoma on the latter is very capricious in its occurrence; in some years it may be found almost everywhere, in other years hardly a specimen can be met with. The large yellow spots show conspicuously on the upper surface of the leaves, so that when it does occur it is impossible to overlook it.

There are two places near Birmingham where all the spore-forms occur year after year in close proximity: it is from these specimens that the descriptions are taken. In one case the teleutospores are on *P. alba*, in the other on *P. tremula*.

The morphological differences of the four (or five) species of *Melampsora* which appear on *P. alba* and *P. tremula* are very slight. It is better to include them all for the present under *Melampsora tremulae*, as biological races. The fourth species is *M. Magnusiana* Wagner, which has its caëmata on *Chelidonium*, and which, according to Klebahn, is identical with *M. Klebahnii* Bubák, on *Corydalis*; this has not yet been recorded for Britain, but Plowright mentions (*l.c.* p. 241) a *Melampsora* on *P. tremula* from which he could not obtain caëmata on either *Larix* or *Pinus* or *Mercurialis*—this might be *M. Magnusiana*.

12. *Melampsora Euphorbiæ* Cast.

Uredo Helioscopiae Pers. Disp. Meth. p. 13.

Lecythea Euphorbiæ Lév.; Cooke, Micr. Fung. p. 221.

Melampsora Euphorbiæ Cast. Obs. ii. 18, with plate (1843). Cooke, Handb. p. 523; Micr. Fung. p. 219, pl. 9, f. 193, 194.

M. Helioscopiae Wint. Pilze, p. 240 (1884). Plowr. Ured. p. 236.

Sacc. Syll. vii. 586. Fischer, Ured. Schweiz, p. 508, f. 318.

[*Spermogones*. Flat, hemispherical.

Æcidiospores. Caëmata minute, $\frac{1}{4}$ — $\frac{1}{2}$ mm. diam. on the leaves, 1—4 mm. long on the stems, yellowish-red; spores in

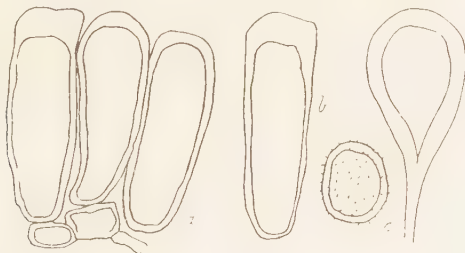


Fig. 264. *M. Euphorbiæ*. a, telutospores on *E. exigua*; b, teleutospore, and c, uredospore and paraphysis, on *E. Peplus*.

short chains, without paraphyses, roundish to ellipsoid, densely verrucose, $21-28 \times 19-24 \mu$.]

Uredospores. Sori hypophyllous and on the stems, scattered roundish or oblong, soon naked, but surrounded by the epidermis, golden-brown, mixed with numerous capitate paraphyses: spores roundish, orange, $15-17 \times 11-14 \mu$; epispore colourless, echinulate, without perceptible germ-pores; paraphyses hyaline, with strongly thickened heads, $16-23 \mu$ diam.

Teleutospores. Sori amphigenous, subepidermal, minute, roundish or oblong, reddish-brown, then black, more or less pulvinate, on the stems often confluent: spores prismatic, $50-60 \times 10-14 \mu$; epispore brown, thin, at length thickened above (up to 5μ) and darker.

On *Euphorbia exigua*, *E. Helioscopia*, *E. Peplus*. May—October. Very common. (Fig. 264.)

Müller, on the ground of cultures, considers the form on *E. Helioscopia* as a separate species from those on *E. Peplus* and *E. exigua*, the latter two also being biologically distinct from each other (Centralbl. f. Bakter. 2. xix. 441). In his experiments he observed a caëma-stage on *E. exigua* which the others did not have. This stage seems to be very rarely met with, and has probably not occurred in this country: the description of the spermatogones and caëmata is from Fischer. In the same species, as it occurs on *E. Cyparissias*, Jacky states that he obtained the uredospores by infection with the basidiospores without the intervention of the caëma-stage, so that *M. Euphorbiae* may be in a transition state between a *eu*-form and a *hemi*-form. The aëcidium on *E. exigua* recorded by Plowright (*l.c.* p. 270) belongs to *Uromyces tuberculatus*; see p. 102.

DISTRIBUTION: Europe, Siberia.

13. *Melampsora Hypericorum* Wint.

Uredo Hypericorum DC. Flor. fr. vi. 81. Cooke, Handb. p. 526;

Mier. Fung. p. 215, pl. 8, f. 174, 175.

Melampsora Hypericorum Winter, Pilze, p. 241. Plowr. Ured. p. 243.

Sacc. Syll. vii. 591. Fischer, Ured. Schweiz, p. 506, f. 317.

McAlpine, Rusts of Australia, p. 191.

Aëcidiospores. Caëmata hypophyllous, scattered, roundish or oblong, flatly pulvinate, often very small, subepidermal, long covered, at length erumpent, orange, showing as indefinite pale-yellow or orange spots on the upper face; spores in short

chains, ellipsoid to polygonal or subclavate, $18-28 \times 10-18 \mu$; épispore colourless, about 2μ thick, rather densely verruculose, with no perceptible germ-pores; no paraphyses.

Teleutospores. Sori hypophyllous, subepidermal, small, roundish, reddish-brown, then dark-brown; spores prismatic, more or less rounded above, pale-brown, $28-40 \times 10-17 \mu$; épispore thickened (up to 3μ) above.

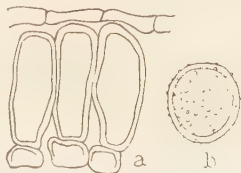


Fig. 265. *M. Hypericorum*. a, teleutospores, under the epidermis; b, æcidiospore, without paraphyses. On *H. Androsæmum*.

On *Hypericum Androsæmum*, *H. humifusum*, *H. perforatum*, *H. pulchrum*. Not common. May—October. (Fig. 265.)

What was described by Plowright as the uredo-stage of this fungus is stated by Fischer, Tranzschel, and others, to be the cœoma stage—the spores “being produced in short chains, with sterile intercalary cells, without paraphyses, but sometimes” (at least on *Hypericum montanum*) “surrounded by a layer of swollen colourless cells which might almost be considered as an undeveloped peridium.” Müller considers the form on *H. montanum* as a biological race, since he could not infect other species of *Hypericum* with spores from it.

But Klebahn has proved (Zeitschr. f. Pflanzenkr. 1905, xv. 106) that a species of *Hypericum* can bear both the cœoma-form without paraphyses and the uredo-form with paraphyses. McAlpine (Rusts, p. 192) records that in Australia the uredo-sori have very abundant paraphyses, intermixed; he describes them as “hyaline, capitate, overtopping the spores, $50-68 \times 18-24 \mu$.” His species was on leaves and stems of *H. japonicum*, and differs slightly from the British ones. His description of the uredo-sori is as follows: “Sori mostly hypophyllous, scattered or gregarious, at first bright-orange, becoming pale, pulverulent, up to $\frac{1}{2}$ mm. diam., erumpent and surrounded by the ruptured epidermis. Spores subglobose to ellipsoid, finely verrucose, orange-yellow, $14-21 \times 11-17 \mu$, with two germ-pores on one face.” On the British specimens which I have seen, there are no paraphyses and the spores are decidedly in chains.

DISTRIBUTION: Europe, Siberia, India.

14. *Melampsora Lini* Desm.

Uredo miniata var. *Lini* Pers. Syn. Fung. p. 216.

U. Lini Schum. Pl. Säll. ii. 230. Arthur, N. Amer. Fl. vii. 101.

Lecythea Lini Berk. ; Cooke, Handb. p. 532 ; Micr. Fung. p. 222, pl. 8, f. 165-7.

Melampsora Lini Desm. Pl. Crypt. no. 2049. Plowr. Ured. p. 237. Sacc. Syll. vii. 588. Fischer, Ured. Schweiz, p. 507. McAlpine, Rusts of Australia, p. 192, f. 236 and pl. I, f. 36.

Spermogones } See below.
Æcidiospores }

Uredospores. Sori amphigenous and on the stems, small, scattered, roundish or oblong, flatly pulvinate, subepidermal, (at first covered by a parenchymatous peridium, Fischer), orange; spores roundish to ellipsoid, echinulate, orange-yellow, $16-24 \times 12-17 \mu$; paraphyses not numerous, hyaline, strongly capitate, much thickened above, $20-25 \mu$ diam.

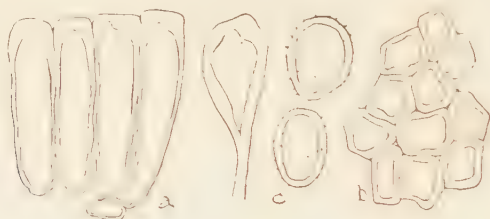


Fig. 266. *M. Lini*. a, teleutospores; b, plan of same; c, paraphysis and two uredospores. On *L. catharticum*.

Teleutospores. Sori similar, but confluent, chiefly on the stems, subepidermal, reddish-brown, at length black and shining; spores prismatic, $35-60 \times 7-10 \mu$; epispore thin, yellowish-brown, rather thickened above and darker.

On *Linum catharticum*. June—October. Not uncommon. (Fig. 266.)

Forms of *Melampsora Lini* occur widely on many species of *Linum* and have usually been regarded as identical. That which often acts as a very destructive parasite wherever the common Flax is cultivated has considerably wider teleutospores ($17-20 \mu$, McAlpine) and attempts to infect *L. usitatissimum* from *L. catharticum* have uniformly failed; it is therefore considered by some as a biological race or even species = *Melampsora liniperda* Körnicke (Centralbl. f. Bakter. 1911, 2. xxxii. 278). Teleutospores of this have been described as much as 80μ long. Fromme (1912) has recently described spermogones and æcidia to this form on cultivated

Flax; the spermogones are flask-shaped, subepidermal, without ostiolar filaments, the aecidia are small and apparently difficult to distinguish. No other author seems to have met with these, unless the structures to which Fischer assigns a "parenchymatous peridium" were such aecidia.

It would keep the disease in check if infected Flax plants were pulled up and burnt as soon as seen, but such a remedy is impracticable on a large scale. No really immune varieties of Flax are known, but fortunately the parasite seems not to occur in the Irish flax-fields.

DISTRIBUTION: Europe, North and South America, Australia.

15. *Melampsora vernalis* Niessl.

Uredo Saxifragarum DC. Flor. fr. vi. 87. Cooke, Handb. p. 525; Micr. Fung. p. 215.

Caecoma Saxifragae Wint. Pilze, p. 258. Plowr. Ured. p. 259.

Melampsora vernalis Niessl, in Wint. Pilze, p. 237 (1881). Plowr. Gard. Chron. 1890, viii. 41; Jour. Roy. Hort. Soc. xii. p. cxi; Trans. Brit. Myc. Soc. i. 59. Sacc. Syll. vii. 592.

M. Saxifragarum Schröt. in Cohn's Krypt. Flor. Schles. p. 375 (1887). Fischer, Ured. Schweiz, p. 511.

Spermogones. Scattered, yellow.

Aecidiospores. Caemata small, elliptic, flat, solitary, golden-yellow; spores in chains, roundish, finely verruculose, 17—30 μ .

[*Uredospores*. Sori epiphyllous, very small, round; spores ellipsoid, echinulate, golden-yellow, 16—20 $\times$ 15 μ .]

Teleutospores. Sori densely clustered, subepidermal, small, irregular, chestnut-brown; spores oblong to clavate, yellowish-brown, 40—50 $\times$ 14 μ .

On *Saxifraga granulata*. Rare. June—September.

Plowright states that, on the specimens collected by Mr James Taylor at Clark Farquhar, N.B., in June, 1890, the teleutospores were found on the lower leaves and stems, and there were no uredospores. The description of the latter is after Voglino and Fischer, and may not belong to the British species. The connection of the caecoma with the teleutospores has been proved by Plowright and Dietel.

DISTRIBUTION: Germany, Switzerland, Italy.

MELAMPSORIDIUM Klebahn.

Heterœcious.

Teliospores one-celled, with brownish membrane, united into flat waxy crusts, but each little group starts almost always directly beneath a stoma. Uredo-sori surrounded by a hemispherical peridium which opens by an apical pore, often beginning beneath a stoma; uredospores abstricted singly, more or less smooth at one end, with indistinct germ-pores, not mixed with capitate paraphyses. Æcidia with a well-developed inflated peridium. Spermatogones subcuticular, other sori subepidermal.

This genus is, in some respects, as closely allied to *Pucciniastrum* as to *Melampsora*, or rather more to the former than to the latter.

Melampsoridium betulinum Kleb.

Uredo populina var. *betulina* Pers. Syn. p. 219.

Melampsora betulina Desm. ; Cooke, Handb. p. 522, f. 212 (misnamed *winter* spores); Micr. Fung. p. 219, pl. 9, f. 189, 190. Plowr. Ured. p. 243. Sacc. Syll. vii. 592.

Melampsoridium betulinum Kleb. Zeitschr. f. Pflanzenkr. 1899, p. 21 (see also 1891, p. 130); Wirtswechs. Rostp. p. 401. Fischer, Ured. Schweiz, p. 512, f. 320.

Æcidiospores. Æcidia hypophyllous, single or in longitu-

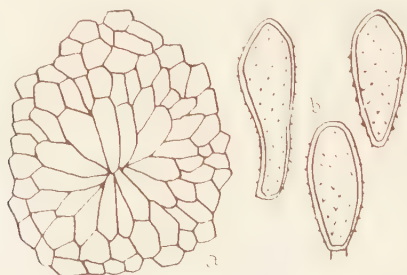


Fig. 267. *M. betulinum*. a, peridium of uredo-sorus, viewed from above, showing the point at which it will dehisce, $\times 300$; b, uredospores, $\times 600$.

dinal rows parallel to the mid-rib, small, oval or oblong, $1-1\frac{1}{2}$ mm. long, clear reddish-orange, with irregularly torn margin;

spores roundish, $14-21 \times 11-16 \mu$, echinulate; episporium thinner and smoother above.

Uredospores. Sori hypophyllous, with yellow spots showing on the upper side, collected in groups and mostly limited by the veins, each sorus scarcely $\frac{1}{12}$ mm. wide, surrounded by a dome-shaped peridium which at length opens at the summit (where its cells are drawn out into long sharp points, Fischer); spores decidedly oblong or subclavate, orange, $22-40 \times 8-12 \mu$; episporium colourless, with distant spines, often smooth above.

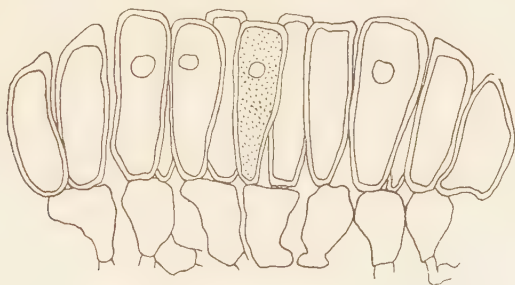


Fig. 268. *M. betulinum*. Sorus of teleutospores. The fusion-nucleus is seen in four of them. $\times 600$.

Teleutospores. Sori hypophyllous, always covered by the epidermis, scarcely $\frac{1}{2}$ mm. wide, in dense clusters limited by the veins, often spread over the whole leaf, reddish, then brown; spores prismatic, rounded at both ends, somewhat oblique, $30-50 \times 7-15 \mu$; episporium thin, scarcely thickened above, nearly colourless, without perceptible germ-pore.

Æcidia on leaves of *Larix europaea*, May; uredo- and teleutospores on *Betula alba* (both *verrucosa* and *pubescens*), August—November, lasting through the winter on the decaying leaves. (Figs. 267, 268; see also Fig. 37, p. 78.)

It was Plowright who first, in 1890 (after many unsuccessful trials) discovered that the Melampsora on Birch was connected with an æcidium-form on Larch (see Zeitschr. f. Pflanzenkr. i. 130; Gard. Chron. 1890, viii. 41). He performed the experiment in both directions, and his conclusions were confirmed, eight years later, by Klebahn. The æcidium in this case does not belong to the *cæoma*-type, but to that of *Peridermium* (*P. Laricis* Kleb.), having a peridium and resembling in its spores also *Peridermium Strobi*. The forms on *B. verrucosa* and *B. pubescens* are, to a small extent,

biologically distinct. The æcidium stage of this parasite is very rare everywhere, and seems not to be recorded in Britain, except by Plowright at King's Lynn; the other stages are exceedingly common all over the country, but do little damage. The teleutospores germinate after a winter's rest, but since it is supposed they cannot infect the Birch and the æcidium-stage appears to be so rare, it is doubtful by what means the fungus propagates itself from year to year. Liro states that in Northern Europe the æcidium on the Larch does not occur, though the fungus is very common in the uredo-stage, especially on Birch seedlings; but as he also says that the uredospores do not survive the winter there, the question of its perennation is left in a very unsatisfactory state.

On the Hornbeam (*Carpinus Betulus*) there is in Europe an allied species (*Melampsoridium Carpini*) to which an æcidium has not yet been discovered.

DISTRIBUTION: Europe, Asia, North America.

MELAMPSORELLA Schröter.

Heterœcious.

Teleutospores in the epidermal cells, with a thin, colourless membrane, usually one-celled, germinating at once on maturity. Uredo-sori furnished with a peridium, and without any paraphyses amidst the spores; uredospores yellow, sessile, produced in short chains or singly, without evident germ-pores. Æcidia with a peridium. Uredo-sori and æcidia subepidermal: spermogones subcuticular; without ostiolar filaments.

This genus bears a certain resemblance to *Milesina* but is distinguished from it by the absence of vertical septa in the teleutospores, as well as by its habitat on Phanerogams.

1. *Melampsorella Caryophyllacearum* Schröt.

Æcidium elatinum A. et S. Consp. p. 121. Plowr. Ured. p. 270.

Peridermium elatinum Link; Cooke, Handb. p. 535; Mier. Fung. p. 194.

Uredo Caryophyllacearum Johnst.; Cooke, Handb. p. 526; Mier. Fung. p. 216.

Melampsorella Caryophyllacearum Schröt. in Hedwig, 1874, xiii. 85. Klebahn, Wirtswechs. Rostp. p. 396. Fischer, Ured. Schweiz. p. 516, f. 522—6.

Melampsora Cerastii Wint. Pilze, p. 242 (1881). Plowr. Ured. p. 247.

Melampsorella Cerastii Schröt. Flor. Schles. p. 366 (1887). Sacc. Syll vii, 596.

M. elatina Arthur, N. Amer. Fl. vii, 111.

Spermogones. Epiphyllous, scattered, conical, honey-coloured.

Æcidiospores. Æcidia hypophyllous, arranged in an irregular row on each side of the mid-rib, erumpent, shortly cylindrical, roundish or compressed, pale orange-red, with torn white margin; spores ellipsoid or polygonal, orange, $16-30 \times 14-17 \mu$; episore thin, densely verrucose.

Uredospores. Sori generally hypophyllous, usually arising beneath a stoma, surrounded by a peridium which slowly opens by an apical pore, small, crowded, pustular, yellow; spores sometimes in short chains, ovoid-oblong or ellipsoid, yellowish, $20-30 \times 16-21 \mu$; episore thin, beset with a small number of pointed warts which are only visible when dry, with an occasional glabrous strip(?), without perceptible germ-pores.

Teleutospores. Hypophyllous, often covering the whole leaf, developed within the epidermal cells, whitish-yellow or pinkish, in little groups in each cell, roundish or flattened, one-celled, $14-21 \mu$; episore smooth, thin; basidiospores globose, nearly colourless, $7-9 \mu$.

Æcidia on leaves of *Abies pectinata*, June—September; uredo- and teleutospores on *Cerastium arvense*, *C. triviale* and its var. *alpestre*, *C. viscosum*, *Stellaria graminea*, *S. media* (more rarely); uredospores from May onwards. Not very common. (Figs. 269, 270.)

In North America it occurs on other species of *Abies*, and on *Alsine* and other species of *Cerastium*; also in Europe on numerous allied species of the subfamily Alsineæ. The teleutospores are developed on those leaves of the second host which live through the winter; they germinate about May and can infect the Silver Fir. There are comparatively few records of the æcidium-stage in this country; it causes small erect



Fig. 269. *M. Caryophyllacearum*. *Peridermium elatinum*, on *A. pectinata* (slightly reduced); a, a leaf, $\times 10$.

witches' brooms on the Fir, the infected buds producing dense clusters of small leaves which are not pseudo-distichous—as in the normal shoots—but spirally arranged, moreover they are not evergreen, but fall off in August. On these leaves the spermogones and æcidia are seen in June; and the æcidiospores infect the second host and produce uredo-sori in 10—14 days. It will be seen that the teleutospores found in spring do not belong to the same generation as the uredospores found in the following summer.

The mycelium of both stages is perennial, so long as the host survives, this being the only known instance of such a state of things; for this reason the parasite can maintain itself on either the Fir or the other host quite independently. On the Fir, it produces in time large cankerous growths. There is some evidence that a specialisation into biological races on different species of *Alsineæ* has begun. In the latter the

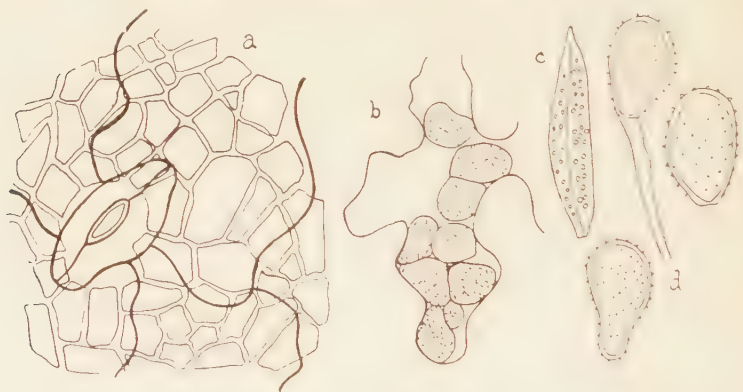


Fig. 270. *M. Caryophyllacearum*. a, cells of the peridium of a uredo-sorus, on *Stellaria graminea*, showing the opening pore being formed beneath a stoma, seen through the epidermis, $\times 600$; b, an epidermal cell of *S. nemorum*, containing teleutospores (after Fischer) $\times$ about 400; c, attacked leaf of *S. graminea*, slightly enlarged; d, one young and two mature uredospores, $\times 600$.

mycelium grows up with the young shoots and gradually spreads upwards into every leaf, making the leaves in many cases smaller, but not much different in colour. I have seen a few uredo-sori on the upper side of the leaves, and even on the sepals of *Cerastium*.

The peridium of the uredospores is formed of a definite hemispherical pseudo-parenchymatous layer, one cell thick, most of the cells being polygonal by mutual pressure, nearly smooth, and containing at first a little of the same yellow oil as the uredospores. It bears a very close resemblance in texture to that round the uredo-sori of *Pucciniastrum Circæe*, *Milosina Blechni*, *Uredinopsis filicina*, and their allies.

The heteræcism of this parasite was established by Fischer in 1901 (*Zeitschr. f. Pflanzenkr.* xi. 321); the result was attained only after a long

and vain search extending over many years; it has been confirmed by Tubeuf, Klebahn, and Bubák. The æcidia of three other species, *Melampsorella Symphyti*, *Pucciniastrum pustulatum* and *Calyptospora Goeppertiana*, which also live on the same host, do not cause any deformation of the shoots, and can therefore be easily distinguished.

DISTRIBUTION: Europe, North America.

2. *Melampsorella Symphyti* Bubák.

Uredo Symphyti DC. Encycl. viii. 232. Plowr. Ured. p. 255. Sacc. Syll. vii. 861.

Trichobasis Symphyti Lév.; Cooke, Handb. p. 529.

Coleosporium Symphyti Fekl. Symb. Myc. p. 43. Cooke, Micr. Fung. p. 218.

Melampsorella Symphyti Bubák, Centralbl. f. Bakter. 2. xii. 423. Fischer, Ured. Schweiz, p. 523.

[*Spermogones*. Chiefly hypophyllous, crowded, often spread over the whole leaf, orange-yellow.

Æcidiospores. Æcidia hypophyllous, in two rows parallel to the mid-rib, not crowded, shortly cylindrical $\frac{1}{2}$ — $\frac{3}{4}$ mm. high, opening at the summit by a cleft, at length torn to the base into 3—5 segments; spores orange, verrucose, $20\text{--}40 \times 18\text{--}29 \mu$.]

Uredospores. Sori hypophyllous, small, rounded, closely crowded, rich golden-yellow, often spread over the whole leaf, at first covered by the epidermis and a thin peridium, then pulverulent; spores ovate or ellipsoid, finely verruculose, yellow, $28\text{--}35 \times 21\text{--}28 \mu$, without evident germ-pores.

[*Teleutospores*. Hypophyllous, developed within the epidermal cells, forming large whitish or pinkish patches, many crowded in each cell, pale-yellowish, smooth, $11\text{--}18 \times 9\text{--}15 \mu$.]

[Æcidia on leaves of *Abies pectinata*, May, June;] uredo-[and teleutospores] on *Symphytum officinale*, rather uncommon, May to September. (Fig. 271.)

Only the uredospores have so far been recorded for Britain, but the teleutospores would in all probability occur on the same plants at a later date, while the æcidia could doubtless be found, if carefully looked for, in

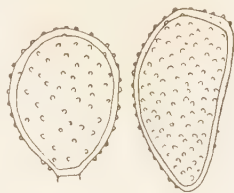


Fig. 271. *M. Symphyti*.
Uredospores, on *S. officinale*.

woods where *Abies* and *Symphytum* both grow together. This was the experience of Bubák (see Ber. Deutsch. Bot. Gesell. 1903, xxi, 356). The teleutospores appear to arise (or at least to mature) about May on a perennial mycelium from the previous year, and are capable of immediate germination: their basidiospores infect the young Fir-needles, but the mycelium thus produced is not perennial and causes no witches'-brooms. The aëdiospores are distinguished from those of the other species which grow upon the same host by their much larger size. The whole of the foregoing particulars except as regards the uredospores are due to Bubák and Fischer; the former found his uredospores chiefly upon *Symphytum tuberosum*.

It will be useful to tabulate here by what characters the various aëcidia on *Abies pectinata* can be discriminated: that belonging to

<i>Melampsorella Caryophyllacearum</i>	causes witches'-brooms.
<i>Melampsorella Symphyti</i>	has large spores $20-40 \times 18-29 \mu$.
<i>Pucciniastrum pustulatum</i>	has a smooth line down the spore.
<i>Calyptospora Goeppertiana</i>	has spores $21-30 \times 14-18 \mu$.

DISTRIBUTION: Europe.

PUCCINIASTRUM Otth.

Heterœcious or aëcidia unknown.

Teleutospores extracellular, in a single layer, subepidermal, with a brownish membrane, divided by vertical septa into 2—4 cells. Uredo-sori surrounded by a delicate hemispherical peridium, opening at the summit with a pore; uredospores yellow in mass, with indistinct or no germ-pores.

Aëcidia with a thin cylindrical peridium (so far as known); aëdiospores verrucose except on one side which is thinner and smooth (? always), not provided with germ-pores.

1. *Pucciniastrum Agrimoniae* Tranzschel.

Uredo Potentillarum var. *Agrimoniae* DC. Flor. fr. vi, 81.

U. Agrimoniae Plowr. Ured. p. 255. Sacc. Syll. vii, 839.

Coleosporium ochraceum Fekl.; Cooke, Micr. Fung. p. 218.

Pucciniastrum Agrimoniae Tranz. Script. Bot. Hort. Petrop. iv, 301.

Fischer, Ured. Schweiz, p. 465. Arthur, N. Amer. Fl. vii, 106.

Uredospores. Sori chiefly hypophyllous, pulvinate, small, confluent, sometimes spread over the whole leaf, covered by the epidermis and surrounded by a thin peridium which opens at the summit with a pore, orange-yellow, fading to ochraceous;

spores shortly ellipsoid or obovate, echinulate, orange, $18-21 \times 14 \mu$; epispore rather thick, with indistinct germ-pores.

[*Teleutospores*. Sori similar, but indefinite, clear-brown; spores subepidermal, extracellular, cuneate, smooth, each divided into four cells by two longitudinal walls at right angles to one another, $30 \times 21-30 \mu$.]

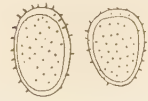


Fig. 272.
P. Agrimoniae.
Uredospores.

On *Agrimonia Eupatoria*. Uredospores common, July—September: teleutospores, very rare everywhere, not yet found in Britain. (Fig. 272.)

We owe our knowledge of the teleutospores to Tranzschel and Dietel; see Engler u. Prantl, *Natürl. Pflanzenfam.* vol. i. pt. 1**, p. 24. Until they were discovered, the position of the fungus was quite uncertain. Klebahn (see *Zeitschr. f. Pflanzenkr.* 1907, xvii. 149) proved that the parasite could maintain itself by over-wintered uredospores.

DISTRIBUTION: Europe, Asia, North and South America.

2. *Pucciniastrum Circææ* Speg.

Uredo Circææ Schum. *Pl. Säll.* ii. 228.

Cooke, *Micr. Fung.* p. 217, pl. 7, f. 135, 136.

Puccinia Circææ Pers.; Cooke, *Handb.* p. 507 p.p.

Melampsora Circææ Winter; Plowr. *Ured.* p. 245.

Pucciniastrum Circææ Speg. *Dec. Myc.* 65. *Sacc. Syll.* vii. 763. Fischer, *Ured. Schweiz*, p. 461, f. 302.

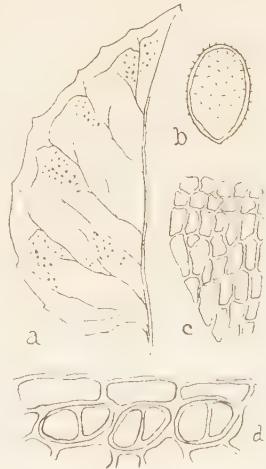


Fig. 273. *P. Circææ*. a, half of a leaf of *C. lutetiana*, showing uredo-sori (slightly enlarged); b, uredospore $\times 600$; c, part of peridium $\times 180$; d, teleutospores, beneath the epidermis, $\times 300$.

Uredospores. Sori hypophyllous, on paler patches bounded by veins, minute, yellowish, crowded, slightly confluent, surrounded by the epidermis and by a peridium which opens at the summit with a pore; spores ovate, $21-24 \times 12-14 \mu$; epispore thin, covered with minute distant warts, without evident germ-pores; paraphyses wanting; peridium usually opening beneath a stoma.

Teliospores. Hypophyllous, in little subepidermal groups, roundish or flattened at the sides, divided longitudinally into about 2—4 cells, $17-24 \times 21-28 \mu$; epispore of uniform thickness (about 2μ), clear-yellowish, smooth.

On *Circaea intermedia*, *C. lutetiana*. Rather common in the uredo-stage. June September. (Fig. 273.)

It is probable that this, like *Pucciniastrum pustulatum*, has an æcidium-stage on a conifer, but nothing has yet been discovered to confirm the suspicion. *Puccinia Circaeae* has sometimes been confounded with this species, though they have nothing in common but the host-plant. They may both be found on the same leaf.

DISTRIBUTION: Central Europe.

3. *Pucciniastrum pustulatum* Dietel.

Uredo pustulata Pers. Syn. p. 219. Cooke, Handb. p. 526; Micr. Fung. p. 215.

Melampsora pustulata Schröt. Pilz. Schles. p. 364. Plowr. Ured. p. 244.

Pucciniastrum Epilobii Oth in Mittheil. Nat. Gesell. Bern, 1861, p. 72.

Sacc. Syll. vii. 762. Fischer, Ured. Schweiz, p. 459.

P. Abieti-Chamaenerii Kleb. Wirtswechs. Rostpilze, p. 393.

P. pustulatum Dietel, in Engler u. Prantl, Nat. Pflanzen. i. 1**, 47. Arthur, N. Amer. Fl. vii. 107.

[*Spermogones.* Hypophyllous, abundant, subcuticular.

Æcidiospores. *Æcidia* hypophyllous, whitish, mostly in two rows corresponding to the two white lines, $\frac{1}{4}$ mm. wide, 1 mm. high, cylindrical, with an evident peridium, opening by longitudinal slits; spores mostly oval, $13-22 \times 10-14 \mu$ ($15-17 \mu$, Dietel); epispore finely verrucose, but with a thinner and smooth area which often forms a longitudinal strip.]

Uredospores. Sori hypophyllous, causing reddish or yellowish spots on the upper surface, roundish, $\frac{1}{4}$ mm. wide, scattered or in little groups, often confluent, orange, surrounded by the peridium and the remains of the epidermis; spores mostly oval, orange-yellow, distantly echinulate, $15-22 \times 11-14 \mu$; paraphyses wanting.



Fig. 274. *P. pustulatum*. *Æcidia* on leaf of *A. pectinata*, slightly enlarged; a, a peridium, $\times 10$. From a foreign specimen.

Teleutospores. Sori hypophyllous, clustered or widely confluent, $\frac{1}{4}$ mm. wide, covered by the epidermis, reddish, then blackish-brown; spores shortly cylindrical or prismatic, $17-35 \times 7-14 \mu$, those in the middle of the sorus *Melampsora*-like, but at the periphery roundish or oval, and composed of 1—3 cells, i.e. divided by longitudinal walls; epispore clear-brown, thickened (up to 3μ) above, but with a thinner spot (! germ-pore).

[*Æcidia* on *Abies pectinata*, June, July;] uredo- and teleutospores on *Epilobium* (*Chamaenerion*) *angustifolium*, *E. palustre*. August—October. Shere, Abinger, Surrey. (Fig. 274.)

The æcidiospores are distinguished from those of *Calyptospora Goepfertiana* by their smooth area and generally shorter length. The æcidium of *Melampsorella Caryophyllacearum* lives also on *Abies pectinata*, but produces thereon witches'-brooms, and finally swellings and canker of the branches, while *P. pustulatum* attacks the leaves only. Klebahn, Fischer, and Tubeuf have all demonstrated experimentally the genetic connection of the stages of this parasite, so far as concerns *E. angustifolium*; but the form on *E. palustre* and its allies is probably, at least biologically, distinct. Klebahn's name, quoted above, includes only the form on *E. angustifolium* and the allied *E. Dodonaei*. He restricts the name *P. Abieti-Chamaenerii* to this, calling the form on *E. palustre*, *E. montanum*, etc. by the name *P. Epilobii*, and assigns to them also certain small morphological differences. The collective species is common in North America, but the æcidium has not yet been recognised there.

DISTRIBUTION: Europe, North America.

4. **Pucciniastrum Pyrolæ** Dietel.

Æcidium Pyrolæ Gmel. in Linn. Syst. Nat. ii. 1473.

Uredo Pyrolæ Grev. Flor. Edin. p. 440 p.p. Fischer, Ured. Schweiz, p. 539, f. 337.

Trichobasis Pyrolæ Berk.; Cooke, Handb. p. 529; Micr. Fung. p. 223 p.p.

Melampsora Pyrolæ Schröt.; Plowr. Ured. p. 247.

Pucciniastrum Pyrolæ Dietel, in Engler u. Prantl, Nat. Pflanzen. i. 1**, 47. Arthur, N. Amer. Fl. vii. 108.

Thecopsora (?) *Pyrolæ* Karst.; Sacc. Syll. vii. 766.

Uredospores. Sori hypophyllous, minute, hemispherical, orange, on yellowish or purplish discoloured spots, surrounded by the epidermis and by a peridium which both open at the

summit with a pore; spores elongated-ellipsoid or clavate, provided with distant and pointed warts, yellowish, $26-35 \times 14-16 \mu$; epispore rather thick, without perceptible germ-pores.

[*Teleutospores*. Sori hypophyllous, adjoining the uredo-sori, inconspicuous, flat, subepidermal, forming an even layer of laterally united cells; spores columnar or oblong, $24-28 \times 10-12 \mu$; epispore colourless, uniformly thin (1μ)—(description after Dietel).]

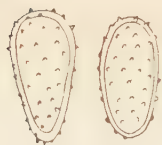


Fig. 275. *P. Pyrolae*.
Uredospores, on *P.*
rotundifolia.

On *Pyrola minor*, *P. rotundifolia*. May—October, uredospores only; Scotland, Ludlow, etc. (Fig. 275.)

Teleutospores have been met with by few observers; previous to their discovery, it was uncertain in what genus the fungus should be placed. It may possibly be heteræcious. The uredospores are often more coarsely warted at one end, though this is not invariably the case. Fischer figures the cells of the peridium round the pore as furnished above with pointed warts, of which one is distinctly longer than the others: those cells are enormously thickened on the lower wall.

DISTRIBUTION: Europe, North America.

THECOPSORA Magnus.

Heteræcious or æcidia unknown.

Teleutospores intracellular, occupying and filling the epidermal cells of the leaves, united into a brown crust, other characters as in *Pucciniastrum*. Uredo as in *Pucciniastrum*. Æcidia hemispherical, with a thick brown peridium (so far as known); æcidiospores verrucose, with a narrow, thin, smooth strip down one side (? always).

1. *Thecopsora Padi* nov. comb.

Licea strobilina A. et S. Consp. p. 109, pl. 6, f. 5.

Pheltonitis strobilina Pers.; Cooke, Handb. p. 409, f. 141.

Perichaena strobilina Fr.; Greville, Scot. Cr. Fl. pl. 275.

Æcidium strobilinum Wint. Pilze, p. 260; Plowr. Ured. p. 266.

Uredo Padi K. et S. exsicc. 187. Cooke, Handb. p. 527.

U. porphyrogenita Kze. ; Cooke, Micr. Fung. p. 216.

Melampsora Padi Cooke, Handb. p. 523 (1871). Plowr. Ured. p. 246. Fung. Fl. Yorkshire, p. 184.

Pucciniastrum Padi Dietel in Eng. u. Prantl, Natiirl. Pflanz. i. 1**, p. 47. Fischer, Ured. Schweiz, p. 463, f. 303; Centralbl. f. Bakter. 2. xv. 227.

Thecopsora areolata Magn. in Hedwigia, 1875, p. 123. Sacc. Syll. vii. 764.

Spermogones. Whitish, pustular, flat, open, exhaling a strong smell.

Æcidiospores. *Æcidia* crowded, covering on the upper (sometimes the under) side the lower part of the scales of the fallen cones, hemispherical or polygonal; peridium thick, brown, woody, opening by a slit; spores oval, inequilateral, yellow, $21-28 \times 17-20 \mu$; epispore very thick (up to 6μ), echinulate, with a narrow, thinner, smooth stripe.

Uredospores. Sori hypophyllous, clustered on spots 1-5 mm. wide which are brownish above, reddish or purplish below, and more or less bordered by the veins, covered by the epidermis and by a peridium which opens at the summit by a pore; spores oblong-oval or irregular, echinulate, pale-yellowish, $15-21 \times 10-14 \mu$; epispore about $1\frac{1}{2} \mu$ thick.

Teleutospores. Developed in the epidermal cells, several in each, epiphyllous or occasionally hypophyllous, forming dark-brown shining crusts which are bounded by the veins; spores oval-cylindrical or prismatic, $22-30 \times 8-14 \mu$, divided by thin longitudinal walls into 2-4 cells; epispore thin, slightly thickened above, clear-brown, smooth, with a germ-pore in the upper and inner corner of each cell.

Æcidia on cones of *Picea excelsa*, Scotland, Yorkshire, August, November; uredo- and teleutospores on *Prunus Padus*, August, September. Very rare. (Fig. 276.)

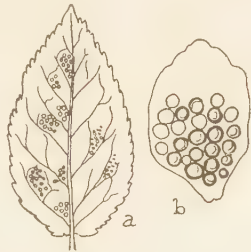


Fig. 276. *Th. Padi*. a, leaf of *P. Padus*, showing uredosori; b, scale of cone of *Picea excelsa*, showing æcidia (both reduced). Some of the æcidia are broken and empty.

The connection of the spore-forms on these two hosts has been experimentally demonstrated by Klebahn, Tubenfl. and Fischer. The basidiospores in spring about the time of pollination of the Fir infect the female flowers of the Spruce Fir, which are usually at the top of the high trees; occasionally also the young shoots are affected, but they do not produce æcidia. The æcidia are developed in late summer, and mature on the fallen cones; their spores germinate in the following May, and then infect the leaves of the Bird Cherry, on which they produce uredospores in the summer and teleutospores in the autumn (Fischer, *l.c.* and *Centrabl. f. Bakter.* 2, xv. 1906, p. 227). The description of the teleutospores is taken from Klebahn and Fischer. As will be seen from the synonymy, the æcidium was originally classed among the *Myxomycetes*. The three stages appear in Cooke's Handbook (according to the knowledge then prevailing) on three different pages, the æcidium from Appin, the uredo from some place in Scotland, and the "*Melampsora*" from Swanscombe, Kent (Cooke, 1865). It is also recorded on *P. Padus* in Yorkshire Fung. Fl. p. 184, while the æcidium is recorded on "pine-cone scales" on p. 369. The uredo has also been found at Braemar, Aboyne, Perth, etc.; and the æcidium in Dumfriesshire.

DISTRIBUTION: Europe.

2. *Thecopsora Galii* De Toni.

Caeoma Galii Link, Sp. Pl. ii. 21.

Melampsora Galii Wint. Pilze, p. 244. Plowr. Trans. Brit. Myc. Soc. i. 53.

Pucciniastrum Galii Fischer, Ured. Schweiz, p. 471, f. 307.

Thecopsora Galii De Toni in Sacc. Syll. vii. 765.

Uredospores. Sori scattered or gregarious, small, round, pulvinate, reddish, covered by the epidermis and by a peridium which opens at the summit with a pore; spores shortly ellipsoid or ovate, sparsely echinulate, orange-yellow, $17-20 \times 14-16 \mu$; epispore colourless, without evident germ-pores.

Teleutospores. Developed in the epidermal cells, forming little dark-brown crusts, crowded, roundish, longitudinally septate into 2-4 cells, $21-24 \times 21-32 \mu$; epispore rather thick, yellowish-brown, smooth, with an evident germ-pore at the upper and inner corner.

On *Galium verum* (H. T. Soppitt), June-September, 1889. Very rare.

It is reported, in continental Europe, as occurring on other species of *Galium*, also on *Sherardia* and *Asperula*.

3. **Thecopsora Vacciniorum** Karst.

Uredo Vacciniorum Link, Sp. Pl. ii. 15. Cooke, Handb. p. 527; Micr. Fung. p. 216.

Melampsora Vacciniorum Schröt.; Plowr. Ured. p. 246.

Pucciniastrum Vacciniorum Dietel, in Eng. u. Prantl, Natürl. Pflanz. i. 1**, 47. Fischer, Ured. Schweiz, p. 467, f. 305.

P. Myrtilli Arthur, North Amer. Fl. vii. 109.

Thecopsora Vacciniorum Karst. Bidr. Finl. Nat. xxxi. 59. Sacc. Syll. vii. 765.

Uredospores. Sori hypophyllous, rather small, scattered or in groups on (sometimes orange) discoloured spots which are visible for some time before the sori appear, long covered by the epidermis, brownish, surrounded by a peridium which opens at the summit with a pore; spores ovate to ellipsoid, sparsely echinulate-verrucose, orange-yellow, $15-16 \times 12-13 \mu$, ($21-28 \times 14-18 \mu$, Fischer).



FIG. 277. *Th. Vacciniorum*. Uredospores on *V. Myrtilus* (Scotland).

[**Teleutospores.** Hypophyllous, developed in the epidermal cells which are filled by them and form little brown indehiscent crusts, pale-brown, divided by longitudinal walls, $14-17 \times 7-10 \mu$; episporium uniformly thin.]

On leaves of *Vaccinium Myrtilus*, *V. Vitis-idaea*. Uredospores only, May—October, Shropshire, Yorkshire, North Wales, Scotland. (Fig. 277.)

The teleutospores are very rare, and can be found only on the dead or fallen leaves. Fischer suggests that this may be a heteroecious species as indeed is most likely the case, though no probable suggestion has yet been made as to the nature of the alternate host. He records it on *V. uliginosum* also; and Arthur on several other species of Vacciniaceæ, in the United States.

DISTRIBUTION: Europe, North America.

CALYPTOSPORA J. Kühn.

Heterœcious. Teleutospores intracellular, occupying the swollen epidermal cells all round the stem of the host for a considerable distance, otherwise as in *Pucciniastrum*. No uredo. Æcidia cylindrical, with a thin peridium: æcidiospores verrucose, without germ-pores, and with no smooth spot.

Calyptospora Goeppertiana Kühn.

Æcidium columnare A. et S. Consp. p. 121, pl. 5, f. 4.

Peridermium columnare S. et K.; Cooke, Handb. p. 535; Micr. Fung. p. 194, pl. 2, f. 27, 28.

? *Æcidium pseudo-columnare* Plowr. Ured. p. 271 (not Kühn?).

Calyptospora Goeppertiana Kühn in Hedwigia, 1869, viii. 81. Sacc. Syll. vii. 766. Kew Bulletin, 1907, p. 1, with plate.

C. columnaris Kühn (1886); Arthur, N. Amer. Flor. vii. 114.

Pucciniastrum Goeppertianum Kleb. Wirtswechs. Rostp. p. 391. Fischer, Ured. Schweiz, p. 466. f. 304.



Fig. 278. *C. Goeppertiana*. Affected branch of *V. Vitis idaea*, Scotland (slightly reduced); a, leaf of *A. pectinata*, b, leaf of *A. Nordmanniana*, with æcidia, Torquay (slightly enlarged).

Æcidiospores. Æcidia hypophyllous, arranged in two long rows parallel to the mid-rib, cylindrical, white, with torn or slit margin; spores ellipsoid, uniformly verrucose, orange-red. $21-30 \times 14-18 \mu$.

Teleutospores. Caulicolous (the fusiform attacked part of the stem being swollen and at first clear-pink, passing into brown), developed in the epidermal cells, densely crowded, prismatic, mostly divided by crossed longitudinal walls into four cells, up to 42μ high; epispore yellowish-brown, smooth, thickened (up to 3μ) at the summit, with a germ-pore at the upper and inner corner of each cell.

Æcidia on leaves of *Abies pectinata*, *A. Nordmanniana*, June—September; teleutospores on stems of *Vaccinium Vitis-idaea*, July—September. England, Wales, Scotland. Very rare. (Fig. 278.)

The life-history has been experimentally demonstrated by Hartig, Kühn, and Bubák. It has been shown that the *æcidia* can be developed in artificial cultures on other species of *Abies* (but not on *Tsuga canadensis* or *Pseudotsuga Douglasii*), though it is not recorded on any of these in natural conditions. Saccardo's citation of "*Abies canadensis*" in the *Sylloge* is probably an error. The teleutospores are recorded also on several other species of *Vaccinium*, including *V. Myrtillus* A. Gray, in the United States, but the *æcidia* have not been observed there.

The infested branches of the Cowberry stand perfectly erect; the plant becomes taller and the leaves stunted. No uredo-stage occurs. For the life-history see p. 59. The mycelium is perennial in the Cowberry, producing fresh crops of teleutospores year after year; this may be the origin of the (presumably) erroneous statement in the Kew Bulletin (*l.c.*) that the basidiospores are able to infect the *Vaccinium* again, as well as the Silver Fir. This statement was originally made by Hartig, but is unsupported by any experimental evidence.

When planting any of the species of *Abies* liable to attack, it would be well to look for and burn all infested bushes of Cowberry in the neighbourhood; they are easily recognisable by their peculiar habit. The fungus cannot attack the Firs unless the infested Cowberry is near enough to convey the infection.

DISTRIBUTION: Europe, North America.

HYALOPSORA Magnus.

Teleutospores in one or two layers, produced in the epidermal cells which are united into crusts; spores with colourless membrane, each divided by vertical septa into 2—4 (or more) cells. Uredo-sori subepidermal, without a peridium or with a very rudimentary one, but surrounded by paraphyses; uredospores of two kinds, yellow, sessile, furnished with evident germ-pores. On Ferns.

It has been suggested that the species of *Hyalopsora* are heterœcious, *Abies* and *Pinus* being named by Bubák (1906) as

possible alternate hosts. This is in itself improbable and is inconsistent with Arthur's suggestion that of the two kinds of uredospores the first kind represents æcidiospores.

1. *Hyalopsora Aspidiotus* Magn.

Uredo Polypodii Schröt. Krypt. Flor. Schles. iii. 374. Plowr. Ured. p. 256 p.p. Sacc. Syll. vii. 857 p.p.

U. Aspidiotus Peck in Ann. Rep. N. Y. State Mus. xxiv. 88.

Melampsorella Aspidiotus Magn. Ber. Deutsch. Bot. Gesell. xiii. 288.

Pucciniastrum Aspidiotus Karsten, Bidr. Finl. Nat. Folk, 1879, xxxi. 143.

Hyalopsora Aspidiotus Magn. Ber. Deutsch. Bot. Gesell. 1901, xix. 582. Arthur, N. Amer. Flor. vii. 112.

H. Polypodii-Dryopteridis Magn. in Hedwig. 1902, p. 224. Fischer, Ured. Schweiz, p. 472, f. 308.

Uredospores. Sori amphigenous, scattered, small, round, up to $\frac{1}{2}$ mm., golden-yellow, without a peridium, dehiscing irregularly, often seated on yellowish spots; spores oblong or ellipsoid, of two kinds, (1) thick-walled ($2\frac{1}{2}$ — $3\frac{1}{2}$ μ), with very



Fig. 279. *H. Aspidiotus*. Part of frond of *P. Dryopteris*, showing uredo-sori, nat. size; three spores, all from the same sorus (Scotland).

faint, hardly perceptible warts, 36 — 72×30 — 40 μ , with 6—8 scattered germ-pores, (2) thin-walled (about $1\frac{1}{2}$ μ), covered uniformly with very faint scattered warts, 28 — 40×16 — 26 μ , with four indistinct equatorial germ-pores; paraphyses few.

Teleutospores. In the epidermal cells, often filling them completely, roundish or irregular, flattened where they are in contact, sometimes arranged in two layers, about 25 μ high, 21 — 35 μ or more wide, divided by vertical septa into 3—5

(mostly four) cells; epispore thin, smooth, colourless; germ-pore not perceptible.

On *Polypodium Dryopteris*. Uredospores, June—August; teleutospores, May and June, on *young* leaves (Magnus). Rare. (Fig. 279.)

Fischer, who records it also on *P. Robertianum*, states that the teleutospores germinate in June. Arthur prefers to call the first kind of uredospore the æcidiospore; this is possibly correct but, until something is known about their development, it is premature to decide. According to him, the æcidia have no peridium, and the uredo-sori a very rudimentary one, but I have repeatedly found both kinds of spores in the same sorus. They appear perfectly smooth, when seen in water.

DISTRIBUTION : Europe, North America.

2. *Hyalopsora Polypodii* Magn.

Uredo linearis var. *Polypodii* Pers. Syn. p. 217.

U. Filicum Desm.; Cooke, Handb. p. 526; Mier. Fung. p. 215 p.p. White, Scot. Nat. 1877, iv. 27, pl. 2, f. 7.

U. Polypodii DC. Flor. fr. vi. 81. Plowr. Ured. p. 256 p.p. Fungus Flor. Yorkshire, p. 204. Sacc. Syll. vii. 857 p.p.

Pucciniastrum Polypodii Dietel, in Hedwig. 1899, xxxviii. 260.

Hyalopsora Polypodii Magn. Ber. Deutsch. Bot. Gesell. 1901, xix. 582.

Fischer, Ured. Schweiz, p. 474, f. 309. Arthur, N. Amer. Flor. vii. 112. Dietel, Annal. Mycol. 1911, ix. 530.

Uredinopsis Polypodii Liro, Uredin. Fennic. 1908, p. 496.

Uredospores. Sori hypophyllous, minute, scattered, bullate, golden-yellow, without a peridium, rupturing irregularly; spores more or less globose or ellipsoid, of two kinds, (1) thick-walled ($2-3\mu$), with very faint warts, $26-38 \times 18-29\mu$, with 6—8 scattered germ-pores, (2) thin-walled ($1-1\frac{1}{2}\mu$), covered uniformly with faint distant warts, $22-35 \times 13-20\mu$, with four equatorial germ-pores.



Fig. 280. *H. Polypodii*. Uredospores, on *Cystopteris fragilis* (Shrewsbury).

Teleutospores. In the epidermal cells, often filling them completely, showing as yellowish-brown spots on the under side of the leaf, densely crowded, divided into 2—4 cells, each about $14-18\mu$ in diam., single cells subglobose; epispore thin, colourless; germ-pore perceptible at the upper end.

On *Cystopteris fragilis* (= *Polypodium fragile* Linn.) and its var. *dentata*. June—September. Rather rare (2700 ft. on Ben Lawers); occurring freely on cultivated *Cystopteris* in fern-cases. (Fig. 280.)

The same remarks may be made about the uredospores of this as of the previous species. In both cases it is not certain that the teleutospores have been found in Britain, and the description is taken from Dietel and Fischer. Dietel has shown (Ann. Mycol. *l.c.*) that infection by the uredospores can be performed easily in a room on *C. fragilis*; time of incubation fourteen days. This would, therefore, be a very convenient species for cytological investigation among the lowest types, but Dietel obtained no teleutospores.

DISTRIBUTION: Europe, North America.

MILESINA Magnus.

Teleutospores intracellular, hyaline, septate. Uredo-sori furnished with a peridium which opens at the summit with a pore; uredospores hyaline, pedicellate, with a thin epispore, but without germ-pores. On Ferns.

1. *Milesina Dieteliana* Magn.

Milesia Polypodii B. White, Scot. Nat. 1877, iv. 162, pl. 2, f. 5. Sacc. Syll. vii. 768.

Mcampsorella Dieteliana Sydow, in Mycoth. Germ. no. 62 (1903).

Milesina Dieteliana Magn. Ber. Deutsch. Bot. Gesell. xxvii. 325 (1909).

Uredospores. Sori hypophyllous, small, round, pustular, clustered loosely in small groups on brown irregular spots, pale-brown; spores colourless, oblong or obovate, strongly but sparsely and irregularly echinulate above, smooth below, $22-30 \times 15-16 \mu$; wall moderately thick ($1\frac{1}{2}-2 \mu$).



Fig. 281. *M. Dieteliana*. Uredospores, on *P. vulgare* var. *serratum* (C. H. Wright). They were enclosed in a thin white peridium.

[*Teleutospores.* Not found in Britain.]

On *Polypodium vulgare* var. *serratum*, Scotland, December, 1906 (C. H. Wright in Herb. Kew). On *Polypodium vulgare*, Dolgelly, May, 1913 (A. D. Cotton). (Fig. 281.)

The genus *Milesia* is now dropped, because it was founded on an imperfect state which might belong to any one of several genera.

2. *Milesina Blechni* Sydow.

Uredo Scolopendrii Fekl.; Plowr. Ured. p. 256 p.p. Sacc. Syll. vii. 860 p.p.

Melampsorella Blechni Syd. Annal. Mycol. 1903, p. 537.

Milesina Blechni Sydow in Mycoth. Germ. no. 877 (1910).

Uredospores. Sori hypophyllous, hemispherical, pustular, $\frac{1}{4}$ — $\frac{1}{5}$ mm. diam., yellowish, loosely scattered on green or brownish leaf-segments, enclosed in a thin white peridium, opening at

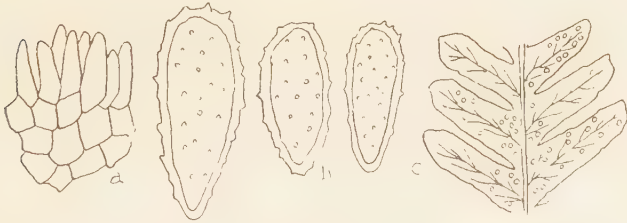


Fig. 282. *M. Blechni*. a, cells of peridium, $\times 360$; b, uredospores, $\times 600$; c, portion of frond of *B. Spicant*, showing uredo-sori, nat. size.

the summit by a round pore which always begins to be formed at a stoma; spores colourless, oblong, obovate or clavate, faintly or irregularly echinulate, $32\text{--}45 \times 12\text{--}18 \mu$; episore $1\frac{1}{2}\text{--}2 \mu$ thick.

[*Teleutospores*. Unknown in Britain.]

On *Blechnum Spicant*. Very uncommon. July—September. (Fig. 282.)

This fungus closely resembles the *Milesina* on *Polypodium vulgare*, and was included under the name *Milesia Polypodii* B. and B. White. The markings on the spores of this and the allied species are more often of the nature of mere roughnesses than like the neat and regular echinulation of the higher types (*Puccinia*, etc.).

3. **Uredo Scolopendrii** Schröt. (probably a *Milesina*).

Ascospora Scolopendrii Fekl. Symb. Myc. Nacht. ii. 19.

Uredo Scolopendrii Schröt. Krypt. Flor. Schles. p. 374. Plowr. Ured. p. 256 p.p. Sacc. Syll. vii. 860 p.p.

U. (?) *Pteridium* White, Scot. Nat. 1877, iv. 27, pl. 2, f. 6.

Milesia Polypodii White p.p.; see Gard. Chron. 1892, 3. xii. 776 (specimen on *Scolopendrium* in Herb. Cooke).

Uredospores. Sori similar to those of *Milesina Blechni*, but larger, about $\frac{1}{4}$ mm., brown, in loose irregular groups; spores

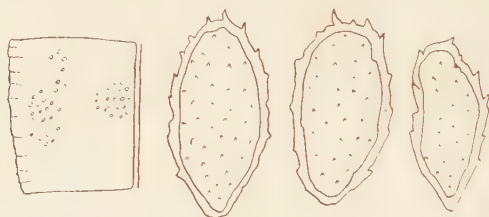


Fig. 283. *U. Scolopendrii*. Portion of frond of *Scolopendrium*, showing sori, nat. size; three uredospores, $\times 600$.

very numerous, oozing out, colourless, clavate, strongly echinate all over, especially at the apex, $35-45 \times 15-23 \mu$; epispore $1\frac{1}{2}-2 \mu$ thick.

On *Scolopendrium vulgare*. Rare; Scotland, England (Cooke), Forden (Rev. J. E. Vize), Warton, N. Lancs., March, 1908 (J. W. Hartley in Herb. Kew). (Fig. 283.)

Only known in the uredo-stage, but closely allied to *M. Blechni*. The name, *Uredo Scolopendrii*, has been used to include many other species.

Besides these parasites on Ferns, Plowright also records under *Uredo Polypodii* (p. 256) a fungus on *Adiantum Capillus-Veneris*. If this is correct, it was probably *Hyalopsora Adianti-Capilli-Veneris* Sydow (Annal. Mycol. 1903, p. 248), which, I am informed by Herr H. Sydow, occurs in Istria and North Italy.

It is quite possible that two others may be found in Britain, viz. *Milesina Kriegeriana* Magn. on *Aspidium spinulosum* and *Uredinopsis filicina* Magn. on *Polypodium Phegopteris*, but I have seen no British specimens. The latter is so likely to occur here, that it is advisable to give a description of it.

UREDINOPSIS Magnus.

Teleutospores solitary, extracellular, hyaline, septate. Uredosori subepidermal, with a distinct peridium; uredospores hyaline, pedicellate, without germ-pores. On Ferns.

This genus is distinguished from all others by the fact that the teleutospores are dispersed without order among the cells of the mesophyll. There are three known forms of spores, which seem to occur simultaneously, and not in a fixed order of succession as in most pleomorphic Uredinales. It is one of the lowest genera from the point of view of organisation: and its cytological investigation would doubtless yield a rich harvest of new ideas.

Not yet discovered in Britain.

Uredinopsis filicina Magn.

Protomyces ? *filicinus* Niessl, in Rab. Fung. Europ. no. 1659, 1873.

Uredo Polypodii var. *Phegopteris* Winter, Pilze, p. 253. Sacc. Syll. vii. 858.

Uredinopsis filicina Magn. Atti Congress. Bot. Internaz. 1892, p. 167.

Fischer, Ured. Schweiz, p. 476, f. 310, 311.

Uredospores. Sori hypophyllous, small, roundish, thickly scattered, yellowish-brown, of two kinds—(1) smaller, about

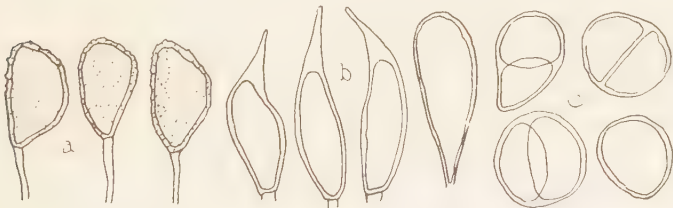


Fig. 284. *U. filicina*. On *P. Phegopteris*. a, uredospores = ? acidiospores; b, uredospores (no. 2) and paraphysis; c, teleutospores. From a German specimen, issued by Sydow.

$\frac{1}{6}$ mm. diam., flattish, semi-transparent, always situated beneath a stoma. surrounded by a rather tough peridium, rupturing above; spores more or less obovate-polygonal, on slender

pedicels as long as or longer than the spore, colourless, densely verruculose, averaging $20-26 \times 12-14 \mu$; epispore about 1μ thick; (2) larger, about $\frac{1}{2}$ mm. diam., more elevated, pustular, without (?) peridium, but with what looked like hyaline clavate thin-walled paraphyses; spores ovate-fusiform, colourless, smooth, thickened at the apex with a conical, acute, usually oblique process, $35-45 \times 10-12 \mu$; pedicels short; epispore thin.

Teleutospores. Scattered singly throughout the mesophyll, i.e. not in definite clusters, roundish-oval or oblong, $1-3$ (mostly two) celled, $18-24 \times 15-16 \mu$; epispore very thin, almost perfectly hyaline and smooth.

On *Polypodium Phegopteris*. Europe. Not uncommon; appearing about the time when the fern-sori are being formed. The uredo-sori are of about the same size as a fern-sporangium, and are scattered among the fern-sori. (Fig. 284.)

The description and figures are taken from a German specimen. The fungus will no doubt be found in this country, if looked for; it is rather conspicuous on account of the uredo-sori. The warts on the uredospores (no. 1) are clearly perceptible even when wet; the peridium is pseudoparenchymatous, with cells isodiametric near the apex, becoming longer and prosenchymatous towards the periphery; texture rather tough and consistent, not friable. Fischer gives a beautiful and accurate drawing of the nature of the peridium and its relation to the epidermis (*l.c.* fig. 310).

The uredospores (no. 2) are described by Arthur in his generic character (*N. Amer. Flora*, vii. 115) as smooth, except for two longitudinal, thickened, more or less warted ridges, which I could not discern.

As in *Hyalopsora*, Arthur prefers to call the two kinds of uredospores respectively acidio- and uredospores: the same remark may be made as under that genus, for the supposed acidiospores occur in company with the teleutospores on the dying parts of the frond, and are said to germinate only after having passed the winter. Uredospores (no. 2) can germinate at once.

The teleutospores are to be found in large numbers in the tissues immediately round both kinds of sori, and simultaneously with them. They are borne on short lateral branches of the mycelium. Dietel, who gave a long account of this fungus (*Ber. Deutsch. Bot. Gesell.* 1895, xiii. 326), showed that in the allied European species, *U. Struthiopteridis*, the teleutospores germinated easily with a typical basidium (occasionally branched) which bore round basidiospores.

DISTRIBUTION: Germany, Switzerland, Italy.

APPENDIX

HEMILEIA Berk. et Broome.

Æcidia, if any, unknown. Uredospores borne singly on hyphæ which protrude in fascicles through a stoma. Teleutospores formed later on pedicels in the centre of the same fascicles, one-celled, with apical germ-pore, germinating as in *Uromyces*.

The character given for *Hemileia*, when only *H. vastatrix* was known, of having one side of the uredospore smooth, is now known to be not of universal application.

Hemileia americana Mass.

Hemileia americana Mass. in Gard. Chron. 1905, xxxviii. 153, f. 53; Kew Bulletin, 1906, p. 40, with plate.

Uredospores. Sori hypophyllous, forming broadly effused pulverulent deep-orange patches, often several centimetres in extent; spores perfectly spherical, shortly stipitate, $24-32\mu$ diam.; epispore bearing small, rather sparsely scattered, round warts, and with two germ-pores.

Teleutospores. Occupying the centres of the heads of uredospores, shortly stipitate, colourless, broadly obovate or turbinate, often with a small obtuse apiculus, densely verruculose, $30 \times 22-25\mu$.

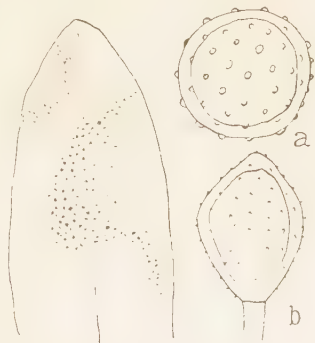


Fig. 285. *H. americana*. Tip of *Cattleya* leaf, showing sori (slightly reduced); a, uredospore, and b, teleutospore, $\times 600$.

On leaves of *Cattleya Dowiana* Batem., imported from Costa Rica, 1899. (Fig. 285.)

Only a small patch of Rust was present on the leaf when the plant was received from Costa Rica, but this continued to increase in size and the falling spores infected other leaves. The uredospores germinated readily, and young *Cattleya* leaves, inoculated on the under surface, produced mature uredospores in thirteen days. No success attended the efforts to infect other orchids, not belonging to the genus *Cattleya*.

This description is founded on that given in the Kew Bulletin; on referring to the Gardener's Chronicle (*l.c.*) it will be seen that the particulars there given differ in several respects. The specimen is in the Kew Herbarium. This fungus and the others of the same genus might easily become dangerous parasites in orchid houses, if allowed to spread; though it seems probable, on the slender evidence at present known, that each is confined, like most other Rusts, to a single genus, if not species.

Hemileia Phaji Sydow.

Uredo Phaji Raciborski, Parasit. Alg. und Pilz. 1900, ii. 32.

U. Lynchii Adams, Irish Naturalist, 1911, xx. 68.

Hemileia Phaji Sydow, Monogr. iii. (ined.). Grove, Journ. Bot. 1913, p. 44.

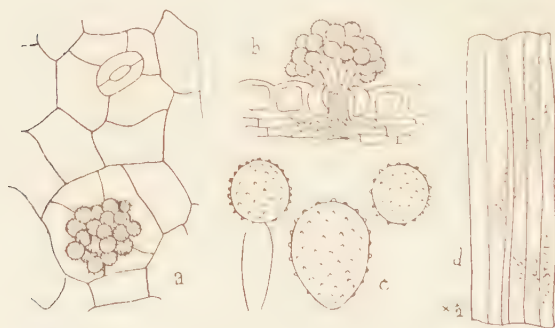


Fig. 286. *H. Phaji*. a, epidermis, showing fascicle of uredospores emerging from a stoma, $\times 180$; b, the same in section; c, uredospores, $\times 600$; d, a portion of a leaf, with uredo-sori, in Herb. Kew, $\times \frac{1}{2}$.

Uredospores. Sori hypophyllous, densely scattered, round, distinct, formed of little dense fascicles of hyphæ (20—25) which issue through a stoma; pedicels divergent, clavate upwards, each surmounted by a spore; spores subglobose or rarely

obovate, strongly but sparsely echinulate-verrucose all over, $13-15\ \mu$ diam. or $18-25 \times 12-16\ \mu$.

On *Phajus Wallichii*. Botanic Gardens, Glasnevin, Dublin (Sir Frederick Moore). April. (Fig. 286.)

The description and figures *a*, *b*, and *c* are derived from some slides mounted by Sir Frederick; I have not seen the leaves, which were not preserved, but there is an exactly similar form on *Phajus* sp. in Herb. Kew, unlocalised but apparently sent up by some gardener for identification. This also was named *Uredo Lynchii* at first.

Hemileia Oncidii Griff. et Maubl.

Hemileia Oncidii Griff. et Maubl., Bull. Soc. Myc. Fr. 1909, p. 138, pl. vi.

Uredospores. Sori hypophyllous, numerous, pulverulent, orange, minute, $50-100\ \mu$ diam.; fertile hyphæ issuing from stomata, fasciculate, branched, $25-30\ \mu$ long, clavate above;



Fig. 287. *H. Oncidii*. Uredospores, *a*, wet, *b*, dry; *c*, part of leaf, showing uredo-sori, $\times \frac{1}{2}$. From the specimen in Herb. Kew.

spores globose or rarely obovate, echinulate-verrucose, filled with orange drops, $16-18\ \mu$ diam., occasionally $20\ \mu$ long; episporium hyaline.

[*Teleutospores*. Sori growing in the centre of the spots, pallid-brownish; spores subglobose or pyriform, at first hyaline, aculeate, then pallid-brown and somewhat smooth, $20-23 \times 15-20\ \mu$.]

On *Oncidium varicosum*, imported by Messrs Stuart Low & Co. from San Paulo, Brazil, August, 1909. Specimen in Herb. Kew. (Fig. 287.)

In the Kew specimen, the spots occupied by the crowded groups of uredo-sori are more or less oval, $\frac{1}{2}-1$ cm. across, and covered with orange-yellow dust, but as the sori are limited, each by the stoma through which it issues, they never become confluent. The description is founded upon that of Griffon and Maublanc; only uredospores were seen. What is doubtless the same species has been found at the Botanic

Gardens, Glasnevin, Dublin, on *Oncidium varicosum* and *O. Forbesii*. Others of the same character were also seen there by Sir Frederick Moore on *Epidendrum vitellinum* and *Lycaete Skinneri*. These tropical parasites are imported with the plants, and occasionally spread to a small extent, under glass, in this country. Persistent examination of such imports would no doubt discover still others of the same kind.

Chrysomyxa Rhododendri De Bary.

Æcidium abietinum A. et S. Consp. p. 120 p.p.

Uredo Rhododendri DC. Flor. fr. vi. 86.

Chrysomyxa Rhododendri De Bary, in Bot. Zeit. 1879, p. 809, pl. 10, f. 1—6. Sacc. Syll. vii. 760. Fischer, Ured. Schweiz, p. 426.

[*Æcidiospores*. *Æcidia* irregular, membranaceous, compressed and elongated parallel to the mid-rib of the leaf (up to 3 mm. long), erumpent on transverse yellowed zones, at length irregularly torn, whitish; spores more or less ellipsoid, yellowish. $17-45 \times 12-22 \mu$; epispore thin, thickly verruculose except for a smooth longitudinal stripe.]

Uredospores. Sori almost always hypophyllous, on yellowish or brownish spots, minute, roundish or oblong, scattered or in small groups, at length pulverulent, orange; spores in chains with intercalary cells, irregular or oval, verruculose, orange-yellow, $17-28 \times 15-22 \mu$, without perceptible germ-pores.

[*Teleutospores*. Sori similar, in densely clustered groups, brownish-red; spores single or in the centre of the sorus several (4—6) superposed in a row, prismatic, $20-30 \times 10-14 \mu$; epispore colourless, thin, but with an annular thickening at the summit of the uppermost cell.]

[*Æcidia* on leaves of *Picea excelsa*, August—October;] uredospores on *Rhododendron hirsutum*, Douglas Castle, Lanarkshire, June, 1913 (D. A. Boyd).

While this book was passing through the press, Mr D. A. Boyd kindly communicated specimens of this most interesting find. It occurred in small quantity, and only uredospores were observed. Description of the other forms after De Bary. This parasite is very common in Switzerland, in all parts where the Fir and the Alpine Roses occur together. The teleutospores germinate in June or July and the spermogones and *æcidia* appear on the Fir leaves from that time onwards. The *æcidiospores* can at once infect the *Rhododendron* leaves, where the mycelium winters,

producing its spores in the following spring. The fungus is recorded also on *R. ferrugineum* and *R. dahuricum*, but does not attack the American or Himalayan species.

DISTRIBUTION: Central Europe, Siberia.

Uredo Lynchii Plowr.

Trichobasis Lynchii Berk. in Gard. Chron. 1877, viii. 242. Berk. et Br. Ann. Nat. Hist. 1878, ser. 5, i. 26. W. G. Smith in Gard. Chron. 1885, xxiii. 693, f. 154.

Uredo Lynchii Plowr. Ured. p. 259. Sacc. Syll. vii. 852.

Uredospores. Sori subepidermal, erumpent, on small pallid spots, scattered, rarely confluent; spores yellow, obovate, beautifully echinulate, with short pedicels, $28-35 \times 20-30 \mu$.

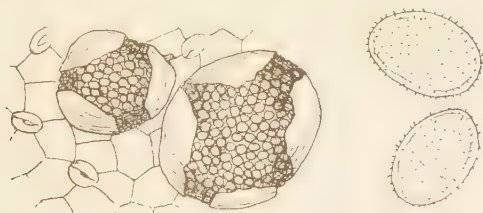


Fig. 288. *U. Lynchii*. Sori on leaf of *Spiranthes*, surrounded by the ruptured epidermis, $\times 40$; two uredospores. From the original specimens.

On a *Spiranthes* from Trinidad, Kew Gardens, August, September; present on the plant when imported (R. Irwin Lynch). On living leaves of *Spiranthes* in hothouse, Kelvinside, Glasgow, September, 1890 (D. A. Boyd). Specimens in Herb. Kew. (Fig. 288.)

Uredo Plantaginis B. et Br.

Uredo Plantaginis B. et Br. Ann. Nat. Hist. ser. 5, vii. 130 (1881). Plowr. Ured. p. 259. Sacc. Syll. vii. 857.

Uredospores. Sori epiphyllous, on round yellowish spots 3—6 mm. wide, erumpent, surrounded by the epidermis; spores roundish to obovate, faintly echinulate with sharp but distant spines, yellowish, varying from $19 \times 20 \mu$ up to $27 \times 16 \mu$, with (apparently) two or three equatorial germ-pores.

On *Plantago lanceolata*(?), *P. major*. Very rare. (Fig. 289.)

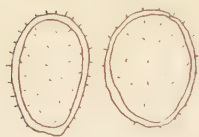


Fig. 289. *U. Plantaginis*.
Uredospores, on *P.*
major, from the Isle of
Wight specimen.

Plowright mentions this with doubt; Berkeley and Broome (*l.c.*) record it as found on *Plantago* at Wood Newton, and on *P. lanceolata* at Dolgelly (Ralfs). In the Trans. Worcester. Nat. Club, 1910, p. 291, it is recorded at Pirton Pool. These I have not seen. Plowright suggests that the Dolgelly specimen may be a *Synechytrium*, and some of those I have seen in herbaria under the name *U. Plantaginis* are not Uredines. But in the British Museum there is one on *P. major*, collected by the Isle of Wight by J. F. Rayner, October, 1907, which appears to belong to this class; the foregoing description is taken from this specimen, the sori lie in the centre of thickened yellow spots which are sometimes confluent.

Uredo Tropæoli Desm.

Uredo Tropæoli Desm. Ann. Sci. Nat. 1836, vi. 243. Cooke, Journ. Bot. iv. 97; Handb. p. 528; Micr. Fung. p. 216. Plowr. Ured. p. 258. Sacc. Syll. vii. 862.

Uredospores. Sori hypophyllous, on pale-yellow spots, minute, roundish, scattered or confluent; spores subglobose to ovoid, orange-yellow, $20\ \mu$ diam.

On leaves of *Tropaeolum aduncum* (= *T. canariense*). Very rare; Shere, near Guildford, October, 1865 (Dr Capron).

This species has been found only once in England. Desmazières who records it on *Tropaeolum minus*, in August, says that it causes, on the upper face of the leaf, numerous irregular spots, barely 1 mm. across. It has been recorded from France and Belgium.

Æcidium Hellebori Fischer.

Æ. Hellebori Fischer, Ured. Schweiz, p. 526

Spermatophores. Epiphyllous, or hypophyllous amongst the acidia, immersed, with projecting paraphyses, about $135-150\ \mu$ diam.

Æcidiospores. Æcidia hypophyllous, crowded, in roundish groups, cup-shaped, with a torn spreading margin; spores densely verruculose, $18-24 \times 18-21\ \mu$.

On *Helleborus viridis*. May.

Included with all reserve. Winter mentions an æcidium on *Helleborus foetidus* (Pilze, p. 269), which he places under *Æc. Ranunculacearum*.

Rev. C. Wolley-Dod records (Journ. Roy. Hort. Soc. xii. p. liii.) an æcidium allied to *Æc. Ficariae* on his Hellebores at Malpas. I have not met with any other reference to an æcidium on that genus. The whole of the description is taken from Fischer, who adds that it belongs presumably to a heterœcious species.

Æcidium Ranunculacearum DC. var. **Linguae.**

Æ. Ranunculacearum DC. Flor. fr. vi. 97 p.p. Grev. Flor. Edin. p. 446. Plowr. Ured. p. 266.

Æcidiospores. *Æcidia* hypophyllous, in roundish or elongated clusters of various sizes, cup-shaped, whitish, with a brittle margin; spores polygonal, orange-yellow, $17-28 \times 14-20 \mu$.

On *Ranunculus Lingua*. Very rare; Duddingston Loch (Dr Greville).

It was at one time suggested by the brothers Sydow that this æcidium belonged to their *Puccinia Calamagrostidis* on *Calamagrostis neglecta*, but they have since seen reason to doubt the truth of this idea.

Æcidium Poterii Cooke.

Æcidium Poterii Cooke, Journ. Bot. ii. 39, pl. 14, f. 3; Handb. p. 540; Micr. Fung. p. 198. Plowr. Ured. p. 268. See also Berkeley, Eng. Fl. v. 373.

Æcidiospores. *Æcidia* hypophyllous, in subrotund or elongated clusters on the nerves of the leaves, also upon the petioles, scattered or circinate, immersed, edges torn into minute fugacious teeth; spores oval, yellowish.

On *Poterium Sanguisorba*. May and June. A species of which nothing else seems to be known.

Æcidium Dracontii Schweinitz.

Æcidium Dracontii Schwein. Trans. Amer. Phil. Soc. 1834. Cooke, Handb. p. 538; Micr. Fung. p. 200. Plowr. Ured. p. 266. Sacc. Syll. vii. 831.

Æcidiospores. *Æcidia* on extensive pallid spots on the leaves, sometimes almost covering them, arranged without order, elongate; spores orange.

On *Arum triphyllum*. In gardens, Melbury, 1863 (Rev. M. J. Berkeley). An introduced species, from North America.

Cæoma Ari-italici Rud.

Uredo Ari-italici Reuquen in Duby, Bot. Gall. ii. 899.

Cæoma Ari Winter Pilze, p. 256.

C. Ari-italici Rud. in Linnæa, iv. 512. Sacc. Syll. Fung. vii. 868.
Trans. Brit. Myc. Soc. i. 60.

Æcidiospores. Cæomata hypophyllous, irregular, flattened, scattered or concentric, often confluent, without a peridium, orange-yellow; spores round or elliptic, often somewhat angular, verrucose, orange, $15-30 \times 15-20 \mu$.

On *Arum maculatum*. Very rare; near Salisbury, April, 1897 (Mr E. J. Tatum). Found also in France and Germany.

Reuquen's description is as follows: *Uredo hypophylla, maculis latis lutescenti-albidis sparsis, acervulis rufis, annulatim digestis, orbicularibus ovatisve, compactis, planis, epidermide rupta cinetis, sporidiis dilute rufis, grossis, pellucidis, subglobosis.*

Phragmidium tuberculatum J. Müller.

This species is recorded for Britain by Sydow (Monographia, iii. 114), on the ground that it was distributed by Baxter, "Stirp. Crypt. Oxon." no. 37. There are specimens of this exsiccatum both at Kew and in the British Museum, but in both these the fungus on Rose-leaves is typical *Ph. disciflorum*, almost all the teleutospores having six septa, not 3—5 as in *Ph. tuberculatum*. The latter species, being widely distributed in Europe, is likely to be found here, but the evidence of its occurrence is at present insufficient.

There is in Herb. Kew an æcidium on "*Atriplex littoralis*, Maldon, Essex, M. A. Irvine," June 1st, 1864. *Æcidia* hypophyllous, covering the whole leaf, densely crowded, shortly cylindrical, with a slightly torn margin. Of this nothing else seems to be known.

EXCLUDED SPECIES.

UROMYCES PARNASSIÆ Cooke, Grevillea, vii. 134. Plowr. Ured. p. 128.

This species does not exist. The æcidium on *Parnassia*, which was at first assigned to it, is now known to belong to *Puccinia uliginosa* (q.v.), and the other stages are merely *Uromyces Valerianæ* on *Valeriana dioica*, as has been pointed out by Sydow. The leaves issued by Cooke under this name (Exsicc. i. 74) are obviously the radical leaves of the Valerian (Fig. 290) which grows in similar places to those suitable for the *Parnassia*. In Sutton Park (Warwicks.) the two plants grow side by side, and when I first found the *Uromyces* there I put it down as *U. Parnassiae*. Rusty marks do frequently appear on the leaves of the *Parnassia* which are placed in herbaria as *U. Parnassiae*, but on examination no spores will be found in them.



Fig. 290. Radical leaves of *Valeriana dioica* (left) and *Parnassia palustris* (right), nat. size.

UROMYCES URTICÆ Cooke, Grevillea, vii. 137. Plowr. Ured. p. 142.

This also is a non-existent species. The origin of the mistake can now never be unravelled.

UROMYCES SCUTELLATUS Cooke, Grevillea, vii. 137. Plowr. Ured. p. 134.

This is probably nothing but an error in identification.

PUCGINIA ASARINA Cooke, Handb. p. 504. Plowr. Ured. p. 202.

This is merely *Puccinia Fergussoni*; the leaves on which the specimens are in Cooke's Exsicc. i. 110 are obviously those of *Viola palustris*. It is rather strange that the spores of this species are exceedingly like the spores of the continental *P. asarina*, and the sori are almost identical in appearance.

PUCCINIA CLANDESTINA Carm. in Berk. Engl. Fl. v. 365, "on *Scabiosa succisa*"; Plowr. Ured. p. 185.

Perhaps the host-plant was mistaken; no *Puccinia* on *Scabiosa* is known.

XENODOCHUS CURTIS Cooke, Micr. Fung. p. 201. Plowr. Ured. p. 228.

Not a Uredine, but may be a species of *Hyphomycetes*.

ÆCIDIUM BARBAREÆ Cooke, Grevillea, x. 115. Plowr. Ured. p. 265.

This record depends, so far as this country is concerned, on a single leaf which was sent to M. C. Cooke by a correspondent, who informed him (on the authority of another person) that the leaf belonged to *Barbarea praecox*. But on examination the leaf is seen to be one of the radical leaves of *Lapsana communis*, of which it has the peculiar hairs, and the fungus is obviously *Æcidium Lapsanae*. The true *Æ. Barbareæ* is quite different. The leaf is preserved in the Kew Herbarium.

ÆCIDIUM INCARCERATUM B. et Br. Plowr. Ured. p. 267.

Plowright's suspicion that this is merely *Doassansia Sagittariae* (on *Sagittaria sagittifolia*) is perfectly correct.

ÆCIDIUM PSEUDO-COLUMNARE J. Kühn.

Recorded in Plowright, Ured. p. 271, on "*Abies pectinata, nordmanniana, amabilis, cephalonica*. Lyme Regis. Mr Munro." Nothing else seems to be known of this as British; most likely the specimens belonged to *Calyptospora Goeppertiana*, or were introduced on imported plants. *Æ. pseudo-columnare* differs from the *æcidium* of *C. Goeppertiana* in having oblong white spores which are larger, more irregular in form, unevenly warted or even smooth at the end (see Hedwigia, 1885, xxiv. 108).

UREDIO OXALIDIS.

There is a specimen bearing this name in the Herbarium of the British Museum, on leaves of *Oxalis Acetosella* (W. Phillips, July 31, 1880) from "Orton"; and a similar one, part of the same gathering, in the Kew Herbarium, from Orton Longueville, Hunts. (Rev. M. J. Berkeley, August, 1880). Both these are not Uredines, but show marks probably of insect-bites.

GLOSSARY

- aculeate.** Covered with needle-like projections.
- alveolate.** Having depressions all over the surface, like a honeycomb.
- amphigenous.** Growing upon both sides of a leaf.
- autœcious.** Having all spore-forms upon the same species of host.
- basipetal.** Having each new part (e.g. spore) formed nearer to the base than the similar preceding one.
- brachymeiosis.** A modification of **meiosis** in which the separation of the chromosomes is not preceded by a contraction of the nuclear material.
- capitate.** Surmounted by a nearly globular head.
- chlorenchyma.** Parenchymatous tissue containing chloroplasts.
- circinate.** Arranged in a circle
- cuneate.** Tapering downwards, with straight sides.
- dendritic.** Having a branched form, like a tree.
- denticulate.** Provided with small teeth-like projections.
- digitaliform.** Having the shape of a finger of a glove.
- echinulate.** Covered with spiny projections.
- ellipsoid.** Having an oval outline, rounded equally at both ends.
- endokaryogamy.** The intracellular fusion of nuclei after a series of conjugate divisions.
- epiphyllous.** Growing on the upper side of a leaf.
- erumpent.** Bursting through the tissues of the host, and becoming superficial.
- fusoid.** Having the shape of a shuttle, tapering at each end.
- gamete.** A cell specialised for reproducing the species, by fusing with another gamete.
- haustoria.** Short mycelial branches which penetrate from the intercellular spaces into the cells of the host, and absorb their nutritive contents.
- heterœcious.** Having some spore-forms upon one species of host and the others upon another species of a different genus.
- hypophyllous.** Growing on the underside of a leaf.
- infection.** The successful attack of the mycelium upon the cells of the host.
- inoculation.** The entry of a germ-tube into a host-plant.

- intercalary.** Occupying a position between other bodies in a row.
- karyogamy.** See **endokaryogamy**.
- lacinate.** Torn into a ragged form at the edge.
- meiosis.** A special type of nuclear division by which the number of chromosomes in each daughter nucleus is *reduced* to half the number present in the nucleus before meiosis.
- metœcious.** The same as **heterœcious**.
- monophyletic.** Descended from a single species or closely allied group of species.
- pallid.** Of the colour of fresh chamois leather.
- paraphysis.** A more or less thread-like organ which grows by the side of the spores.
- plectenchyma.** A kind of pseudo-parenchyma, formed by a mass of intertwined hyphæ.
- polyphyletic.** Descended, in distinct lines, from widely different ancestors.
- pulverulent.** Having a powdery appearance from the loose spores.
- pulvinate.** Having the shape of a cushion.
- punctate.** Marked with little dots, like pin-pricks.
- punctiform.** Having the form of a small pin's head.
- reticulate.** Covered with a network of lines.
- scrobiculate.** Having the surface hollowed out into little shallow pits.
- semi-apogamy.** A fusion of cells for reproduction, where one at least of the fusing cells is still more or less sexually specialised, but the cells are not of opposite sexes. If both cells represent female gametes, it may be called **parthenogamy**.
- trichogyne.** A long hair-like projection from a female cell, suitable for arresting a passing male cell.
- truncate.** As if cut off at the top, with rather square corners.
- verrucose.** Warted, i.e. covered with rounded elevations.
- verruculose.** Covered with minute rounded elevations.
- viable.** Able to put forth a germ-tube.

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